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CONTRIBUIÇÃO PARA O
CONHECIMENTO DA
FAUNA DO KIMERIDGIANO
DA
MINA DE LIGNITO GUIMAROTA
(LEIRIA, PORTUGAL)
III PARTE

V — UPPER JURASSIC LIZARDS FROM CENTRAL PORTUGAL

by

JUERGEN SEIFFERT

VI — TEETH OF ORNITHISCHIAN DINOSAURS FROM
THE UPPER JURASSIC OF PORTUGAL

by

RICHARD A. THULBORN

VII — CHELONIA FROM THE UPPER JURASSIC
OF GUIMAROTA MINE (PORTUGAL)

by

H. BRÄM

LISBOA
1973

TEETH OF ORNITHISCHIAN DINOSAURS FROM THE UPPER JURASSIC OF PORTUGAL

WITH DESCRIPTION OF A HYPsilOPHODONTID
(*PHYLLODON HENKELI* GEN. ET SP. NOV.)
FROM THE GUIMAROTA LIGNITE

by

RICHARD A. THULBORN (*)

INTRODUCTION

The only comprehensive study of the dinosaurs of Portugal is that by LAPPARENT and ZBYSZEWSKI (1957). These authors recognized four Portuguese representatives of the order Ornithischia («ordre des Avipélviens»), namely:

Omosaurus armatus OWEN 1875.

Omosaurus lennieri NOPCSA 1911.

Lusitanosaurus nasicus LAPPARENT & ZBYSZEWSKI 1957.

Iguanodon mantelli MEYER 1832.

Both species of *Omosaurus* come from the Upper Jurassic and they are usually regarded as relatives of the North American *Stegosaurus* on account of their spiny (and possibly plate-like) dermal armour. LUCAS (1902) pointed out that the name *Omosaurus* is preoccupied (having been applied by LEIDY in 1856 to a crocodilian) and suggested the replacement name *Dacentrurus*. The first two ornithischians listed above should therefore be referred to as *Dacentrurus armatus* (OWEN, 1875) and *D. lennieri* (NOPCSA, 1911).

Lusitanosaurus is a problematical form which is known from a single jaw fragment. This specimen cannot be referred with absolute certainty to any particular horizon; but LAPPARENT and ZBYSZEWSKI (1957) have inferred, from the evidence of matrix adhering to the holotype, that *Lusitanosaurus* is probably Lower Jurassic (? Sinemurian) in age. These authors regard *Lusitanosaurus* as an ally of *Scelidosaurus*, an armoured ornithischian from the English Lias (see OWEN, 1861a, 1862; NEWMAN, 1968). Unfortunately the systematic position of *Scelidosaurus* is far from clear; this dinosaur has often been allied with the stegosaurs (for example by SWINTON, 1934, and by ROMER, 1956) but it has recently been compared with the ankylosaurs (ROMER, 1968). It does not seem possible to determine the systematic position of *Lusitanosaurus* until the relationships of *Scelidosaurus* have been clarified.

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The Lower Cretaceous *Iguanodon mantelli* is the only ornithopod which has yet been reported from Portugal.

These four ornithischians are represented by a small number of relatively large specimens. The apparent rarity of ornithischian material may be attributed to two factors:

- 1) Prevalent collecting conditions. The main sources of dinosaur material are coastal exposures — where large and conspicuous fossil bones, which are resistant to wave action, persist on the beaches whilst many smaller fossils are destroyed. KÜHNE (1968) concludes that «...the whole of the Lusitanian (*) is rife with fossil bones but they can be observed and collected only under optimal conditions...».
- 2) The persistence of traditional collecting techniques. Searching by eye and breaking up promising rock has tended, once again, to yield small numbers of large specimens.

This paper deals with ornithopod teeth from the Upper Jurassic rocks of Portugal. These teeth have come from three localities: Porto Pinheiro, Guimarães and Pedrógão (see the maps provided by KÜHNE, 1968, and by SEIFFERT, 1970). Each locality is at a different stratigraphic level. The Pedrógão horizon is probably of Callovian age whilst the Guimarães fossils have been dated as early Kimmeridgian. The Porto Pinheiro specimens seem to be a little younger than those from Guimarães and are probably late Kimmeridgian in age. These various dates are based on the evidence of microfossils.

The numerous specimens forming the basis for this study (218 teeth) are the product of an intensive search which employed several specialized techniques. Material from all three localities was collected and concentrated by the «Henkel method» (see HENKEL, 1968). Details of this screening process have also been described by KÜHNE (1968). The Guimarães and Porto Pinheiro materials were further concentrated by the use of heavy liquids (a technique explained by KERMACK, LEES & MUSSETT, 1965). The material from Pedrógão was also concentrated by means of the photoelectric separation technique described by KÜHNE (1971). Material from all three localities was sorted by hand-picking under a binocular microscope.

Though the material which is described below is very fragmentary it amplifies knowledge of European ornithischians to a considerable degree. The material represents four genera and permits critical reappraisal of the history of the ornithischians in the family Hypsilophodontidae. The ornithischian teeth from Pedrógão, Guimarães and Porto Pinheiro are considered in turn.

THE PEDRÓGÃO ORNITHISCHIAN

Alocodon kushnei gen. et sp. nov.

LOCALITY

Map reference: Carta Militar de Portugal, Sheet 272 (Vieira de Leiria), 0° 11' E., 39° 55' N. The locality is a small pit south of the coastal village of Pedrógão. Here the beds dip to the south-west and form a natural sea wall which shields the exposure. The fossiliferous rocks are soft grey and brownish-grey marls.

(*) The term Lusitanian was coined by CHOFFAT (1885) to cover the late Oxfordian and early Kimmeridgian rocks of central Portugal. In later work (KOBY & CHOFFAT, 1904-5) it was admitted that this name had little more than local significance and I have followed ARKELL (1956) in dispensing with the term Lusitanian.

FLORAL AND FAUNAL LIST

PLANTAE

Chareae:

Porochara sp. (oogonia)*Praschava* sp. (oogonia)

PROTOZOA

Foraminifera:

Fronicularia sp.*Lenticulina* sp.*Nodosaria* sp.

MOLLUSCA

Gastropoda:

3 genera (very common)

Lamellibranchia:

Trigonia sp. (single valve)*Unio* sp.

ARTHROPODA

Ostracoda:

Bisulcoecypria spp.*Cythereella* sp.*Dorcinula* sp.*Kleina* sp.*Lophocythere* *composita**Lophocythere* cf. *flescoata**Monoceratina* *trepti**Monoceratina* aff. *angulata**Schuleridea* sp.*Theriosynocum wyomingense* var. *pedrogavense*

PISCES

Selachii:

Asteracanthus sp.*A. smalli* hybodontid

Holostei:

Caturus sp.*Lepidotes* sp.*Proscinetes* (*Afterodon*) sp.

AMPHIBIA

Urodela

REPTILIA

Chelonii:

Shell fragments

Squamata:

A. kuehneosaurid

Another lizard (jaw fragment)

Crocodilia:

Goniopholia sp.

Another genus

Saurischia:

Theropod teeth

Ornithischia:

Alouidon kuehnei gen. et sp. nov.

Pterosauria:

Rhamphorhynchus sp. (teeth)

The ostracods include cosmopolitan marine types and direct comparisons with ostracod faunas elsewhere in Europe indicate an Upper Callovian age for the Pedrógão horizon.

THE ORNITHISCHIAN TEETH

The Pedrógão locality has yielded 158 ornithischian teeth. Eleven of these were collected during preliminary investigations in 1960; the others were collected in 1970. The teeth are black or dark brown in colour and most are rolled and somewhat damaged. Every example lacks the root. In a few instances the root seems to have been lost

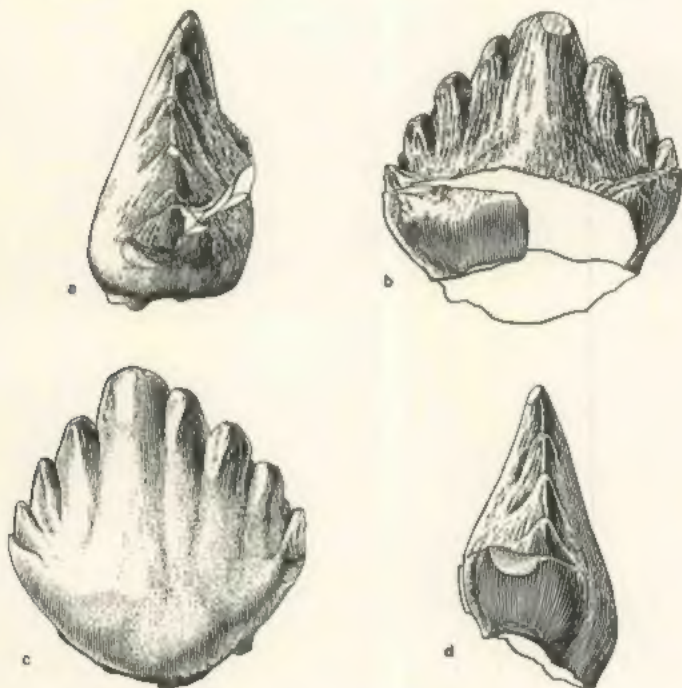


Fig. 1—*Alocodon kushnei* gen. et sp. nov. Holotype. Crown of a cheek tooth in medial (a), lingual (b), buccal (c) and distal (d) views. $\times 14$.

through breakage, but in most cases the base of the crown is excavated into a crater which is marked with fine pits. This pitting may be interpreted as evidence of root resorption and it implies that most of the Pedrógão specimens are shed crowns. At least 20 % of the crowns bear distinct wear facets and many others have blunted margins. These worn surfaces indicate that the teeth were once functional and that they are not just replacement crowns freed by post-mortem decay.

The teeth vary considerably in size and in proportions (see fig. 13). Despite this diversity there are good reasons (discussed below) to assume that the teeth represent a single species of ornithischian dinosaur.

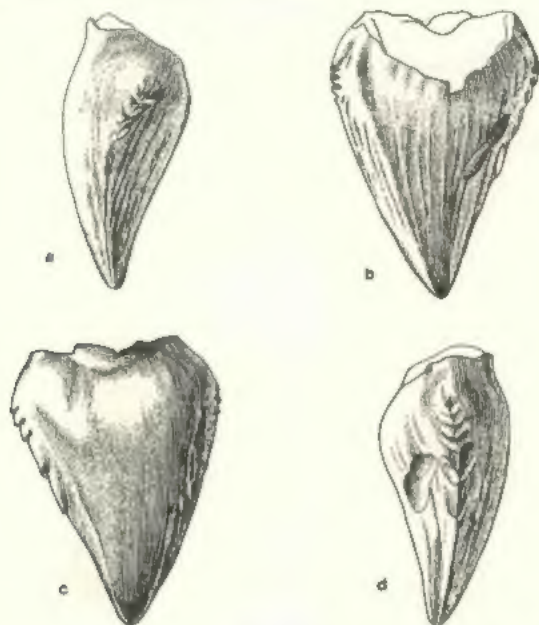


Fig. 2—*Allocodon kuehnei* gen. et sp. nov. Designated paratype. Crown of a tooth from the middle part of the right premaxilla in mesial (a), lingual (b), buccal (c) and distal (d) views. $\times 14$.

SYSTEMATICS

Class REPTILIA

Order ORNITHISCHIA

Suborder ORNITHOPODA

Family HYPSILOPHODONTIDAE

Genus *Allocodon* gen. nov.

Species *A. kuehnei* sp. nov.

Etymology: Greek *σπέρμα* (a furrow) and *ὀδόν* (tooth), in allusion to the ornament of ribs and furrows on the lingual sides of the teeth. The specific epithet is to honour Professor W. G. KÜHNE, whose endeavours secured the material described in this paper.

Type material: The holotype is a single cheek tooth crown (numbered P \times 2). A single premaxillary tooth crown (numbered P \times 1) is designated paratype.

Referred material: The hypodigm of *Alocodon kuehnei* comprises the holotype and the designated paratype together with 156 teeth or parts of teeth. All these specimens are preserved in the collection of the Lehrstuhl für Paläontologie at the Free University, Berlin.

Horizon and locality: All specimens were collected from marls of Upper Cretaceous age near the village of Pedrógão, west coast of Portugal.

Diagnosis (for genus and monotypic species): Ornithischian dinosaur with heterodont dentition. Tooth crowns fully and uniformly enamelled, with smooth and inflated buccal surfaces; lingual surfaces ornamented with fine vertical ribs. Anterior premaxillary crowns tall, acutely conical, recurved, often with shoulder-like swelling of distal margin near cervix. Posterior premaxillary crowns similar, but with small denticles on distal margin (sometimes on mesial margin in addition). Cheek crowns triangular in profile, about as high as long, with occlusal tip formed by a single large denticle; lingual ribbing often irregular; mesial and distal edges with large bluntly rounded denticles; lingual surface with short cingulum near distal margin, sometimes with cingulum near mesial margin in addition. Posterior cheek crowns depressed, much longer than high, but still with large marginal denticles; cingula weak or absent. All cingula irregular, often elaborated into small denticles.

DESCRIPTION (*)

The premaxillary crowns are readily identified by virtue of their conical form and are described first. The maxillary and mandibular crowns cannot be separated (except through their patterns of wear) and the remainder of the description refers to «cheek



Fig. 3—*Alocodon kuehnei* gen. et sp. nov. Lingual (a) and buccal (b) views of a crown from the anterior part of the left premaxilla. Scale indicates 1 mm.

(*) No standard descriptive nomenclature has yet been devised for reptilian teeth. The descriptions involve terms used in human odontology. The tooth surface directed outwards, towards the lips, is termed *buccal*; the surface facing inwards, towards the tongue, is *lingual*. That tooth surface facing the jaw symphysis is *mesial* whilst the opposite surface, directed towards the jaw articulation, is *distal*. The line of junction between root and crown is the *cervix*. The tip of the root is the *apex* of the tooth and structures or surfaces directed towards it are termed *adapical*; the other, masticatory, end of the tooth is defined as *occlusal*.

The following terms also require definition: *crown height* (a maximum adapical-occlusal measurement), *crown length* (a maximum mesio-distal measurement), *crown width* (a maximum bucco-lingual measurement). The *denticle count* expresses the number of marginal denticles on any crown in two figures. The first figure refers to denticles on the mesial margin, the second figure to those on the distal margin. *N. B.* The denticle count does not include the denticle which forms the occlusal tip of the crown.

teeth» in general. Every crown in the heterodont dentition of *Alocodon kuchnei* seems to have been fully and uniformly enamelled.

Crowns from the front of the premaxilla (figs. 3 and 4) are tall, acute and recurved cones which are gracefully arched to the exterior. Each crown is bucco-lingually compressed and is weakly constricted at the cervix. In buccal or lingual view the mesial margin forms an uninterrupted curve (convex forwards); the distal margin forms a corresponding curve but frequently swells, near the cervix, into a pronounced «shoulder». Both mesial and distal edges tend to a definite sharpness as they are traced away from the cervix. The lingual surface is appreciably flatter than the buccal

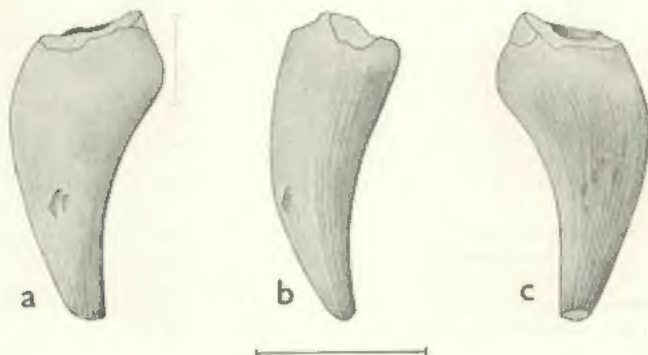


Fig. 4—*Alocodon kuchnei* gen. et sp. nov. Buccal (a), distal (b) and lingual (c) views of a crown from the anterior part of the left premaxilla.
Scale indicates 1 mm.

surface and bears a very characteristic ornament of vertical ridges. Near the cervix these ridges are numerous and ill-defined, but towards the occlusal tip of the crown they converge, decrease in number and become much sharper. The buccal surface, in contrast, is practically smooth. Every crown in the dentition of *Alocodon kuchnei* shows this striking difference between the glabrous buccal face and the ridged lingual face. The Pedrógão material includes at least 21 anterior premaxillary crowns; these range in height from 1.4 mm to 5.0 mm (estimated).

Another premaxillary crown (fig. 5c) bears a small flattened denticle on the lingual face of its inflated distal «shoulder». A second example carries at least five such denticles (fig. 5a), though these are little more than local swellings of the vertical ridges on the lingual surface. These clusters of denticles are present in most of the premaxillary crowns and may be regarded as rudimentary versions of the partial cingula which occur in the cheek teeth (see below). The crown shown in fig. 5a is also of interest in that it has a few marginal denticles; these are located on the distal edge, close to the cervix. The rest of the distal edge, like the entire mesial edge, is devoid of denticles. At least 4 such partly denticulate crowns are present in the material; they range in height from 2.0 mm (estimated) to 4.0 mm and have denticle counts of 0:1, 0:2, 0:3 and 0:5. These partly denticulate crowns probably come from the central part of the premaxilla (i. e. they are transitional between the non-denticulate anterior teeth and the fully denticulate teeth behind).

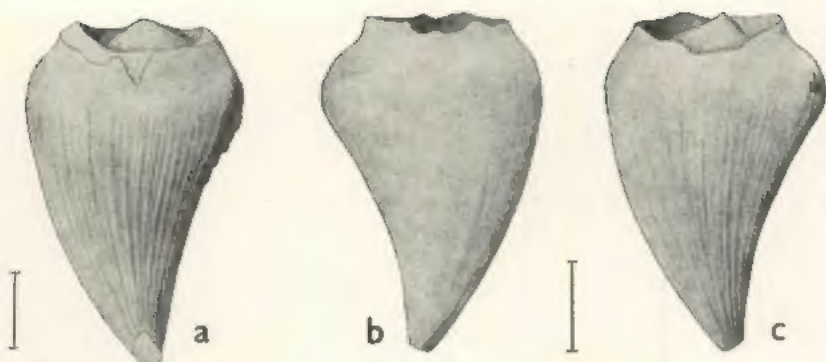


Fig. 5—*Alocodon kuehnei* gen. et sp. nov. Lingual view of crown from the middle part of the right premaxilla (a). Buccal and lingual views (b, c) of a crown from the anterior or middle part of the right premaxilla. Both scales indicate 1 mm.

Crowns from the rear of the premaxilla are somewhat lower and longer than those described above—though they are still higher than long. They are further distinguished by having denticles on both mesial and distal edges (fig. 2). There are at least 10 such crowns in the material; their heights vary between 1.0 mm and 3.6 mm (estimated) and the best-preserved examples have denticle counts of 1:2, 1:3, 2:2, 3:2, 3:3 and 3:4.

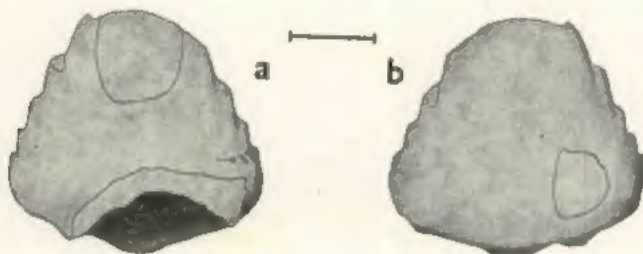


Fig. 6—*Alocodon kuehnei* gen. et sp. nov. Lingual (a) and buccal (b) views of a crown from the anterior part of the left maxilla. Scale indicates 1 mm.

Crowns from the anterior and middle cheek regions (figs. 1, 6, 7, 8 and 9) are about as long as they are high. They appear in buccal or lingual view as broadly rounded and almost bilaterally symmetrical triangles. In each case the occlusal tip of the crown consists of a single large denticle and both mesial and distal edges are elaborated into several smaller, bluntly rounded and slightly irregular denticles. The marginal denticles are usually rather variable but in a few crowns they show a definite decrease in size towards the cervix (fig. 6). In every anterior and middle cheek crown of *Alocodon kuehnei* the most distal of the marginal denticles merges with a short cingulum on the lingual surface. And in the great majority of these crowns there is a similar, but

weaker, cingulum at the mesial margin (fig. 7). In one or two exceptional cases an almost unbroken cingulum extends across the lingual face of the crown (fig. 9). The cingula are somewhat irregular and are frequently developed into lines of small den-



Fig. 7—*Alocodon kuehnei* gen. et sp. nov. Lingual (a) and buccal (b) views of a crown from the anterior cheek region. Scale indicates 1 mm.

ticles. In a few of the larger crowns (such as the holotype) each cingulum is composite, being built of several small «steps» in the crown surface. Most cheek crowns have their lingual faces ornamented with ribs which are less regular and less persistent than those seen in the premaxillary crowns. The material includes at least 31 an-



Fig. 8—*Alocodon kuehnei* gen. et sp. nov. Lingual view of a crown from the middle cheek region. Note that the distal cingulum (at right) is better developed than the mesial one. Scale indicates 1 mm.

terior and middle cheek crowns; these range in height from 1.9 mm to 4.4 mm and have denticle counts such as 3:4, 4:4, 5:4, 5:5, 5:6, 6:5 and 6:6.

The hindmost cheek crowns are much longer than high and bear a superficial resemblance to the teeth of certain hybodontid sharks. Some examples retain cingula at both mesial and distal margins (fig. 10a); others, presumably from farther back

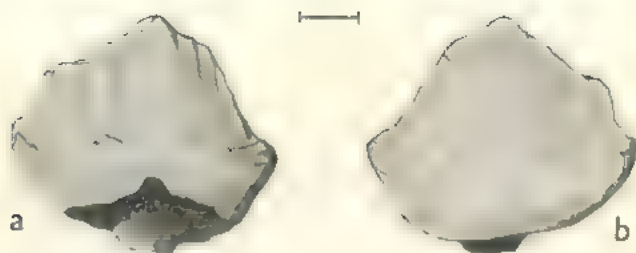


Fig 9 *Alorodonta kuehnei* gen. et sp. nov. Lingual (a) and buccal (b) views of a crown from the middle part of the right dentary. Scale indicates 1 mm.

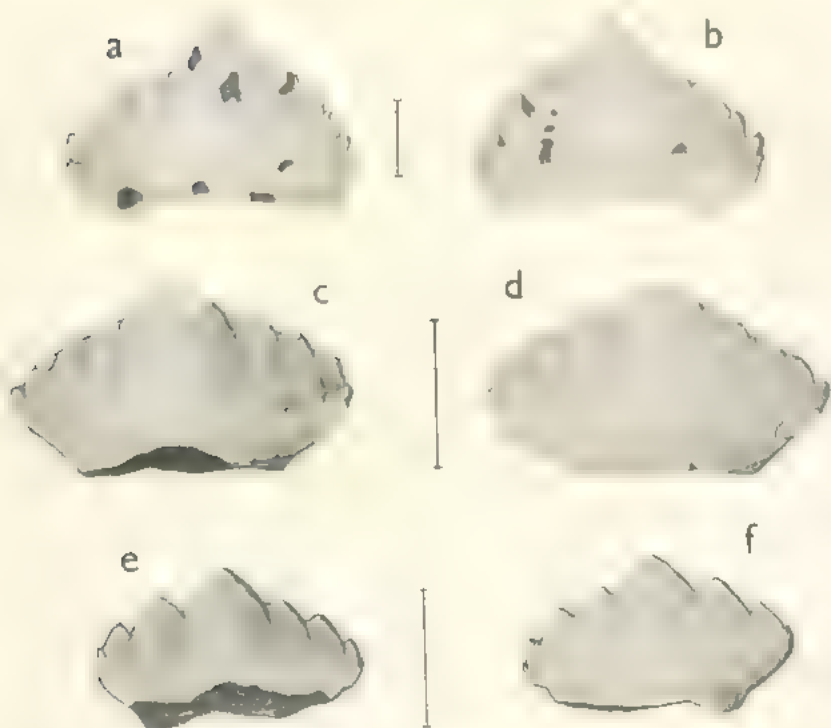


Fig 10 *Alorodonta kuehnei* gen. et sp. nov. Lingual views (a, c, e) and buccal views (b, d, f) of three crowns from the posterior cheek region. Each scale indicates 1 mm.

in the jaws bear only the distal cingulum (fig. 10e). Minute crowns from the posterior extremity of the tooth series have no cingula (fig. 10e). The posterior cheek crowns are represented by at least 15 good examples, these range in height from 0.8 mm to 3.0 mm (estimated) and have denticle counts such as 2 3 3 3 4 4 5 4 and 5 5.

DISCUSSION

Systematic position

Alocodon kuchnei is clearly an ornithischian dinosaur. Its triangular and denticulate cheek teeth are typically ornithischian in appearance and are unlikely to be confused with the teeth of any other reptiles. The well-differentiated premaxillary dentition warrants assignment of *Alocodon kuchnei* to the family Hypsilophodontidae. Premaxillary teeth do occur in a few ornithischians apart from hypsilophodontids — in pachycephalosaurids in protoceratopsians and in the iguanodontid *Thescelosaurus edmontensis* (see STERNBERG 1940 and GALTON 1971) — but these dinosaurs are all as far as I am aware of Upper Cretaceous age. The heterodont dentition of *Alocodon kuchnei* finds convincing counterparts in a number of hypsilophodontids in the late Triassic *Fabrosaurus australis*, in the Upper Jurassic *Echinodon beckhami*, and in the Lower Cretaceous *Hypsilophodon farni*. General similarities between *Alocodon kuchnei* and *Fabrosaurus australis* are particularly noteworthy. One most striking resemblance concerns the transition from the premaxillary dentition to the maxillary dentition in both animals this transition involves a change in tooth crown proportions (i.e. an increase in crown length relative to crown height) and the same gradual acquisition of marginal denticles (first on the distal edges of the crowns, then on their mesial edges). In other hypsilophodontids this changeover from premaxillary to maxillary teeth is achieved in different ways: it is often more abrupt and may even be emphasized by a short diastema (as it is in *Hypsilophodon farni*).

It is important to note that the teeth of *Alocodon kuchnei* may be distinguished from those of any other hypsilophodontid through their finely ribbed lingual faces. The relationships of *Alocodon kuchnei* within the family Hypsilophodontidae are examined more closely in the general discussion (page 118).

Structural variation in the dentition

It has been assumed that the ornithischian teeth from Pedrogão represent a single species. There are several reasons for this assumption. First there are general resemblances between all the tooth crowns: they are all black or dark brown in colour they all appear to have been fully enamelled and they all (where the apical surface is unlamaged) show traces of root resorption. Second and more important, unusual and diagnostic details of tooth structure are evident in nearly every crown, these details include the denticulate cingula and the lingual ornament of ribs. The lingual ribbing is better marked in some crowns than in others, but in no case is it entirely absent. Third the teeth from Pedrogão seem to represent a single well-defined group when they are submitted to simple quantitative analysis. Measurements of maximum crown height and maximum crown length provide distributions approximating to normal (figs. 11 and 12), whilst a simple plot of crown height against crown length produces an acceptably coherent scatter (fig. 13). Finally it is not irrelevant to note that a selection of crowns from the hypodigm of *Alocodon kuchnei* can be fitted together to produce a realistic dentition (fig. 16).

It is not unreasonable to assume that crowns of various shapes and with various styles of marginal denticulation come from different sites within the jaws of *Alocodon*

leuckneri. To investigate this proposition (which is implicit in the description and the diagnosis of the species) I divided the crowns from Pedrógão into 5 groups on the basis of shape (i.e. crown height relative to crown length) and of the distribution of mar-

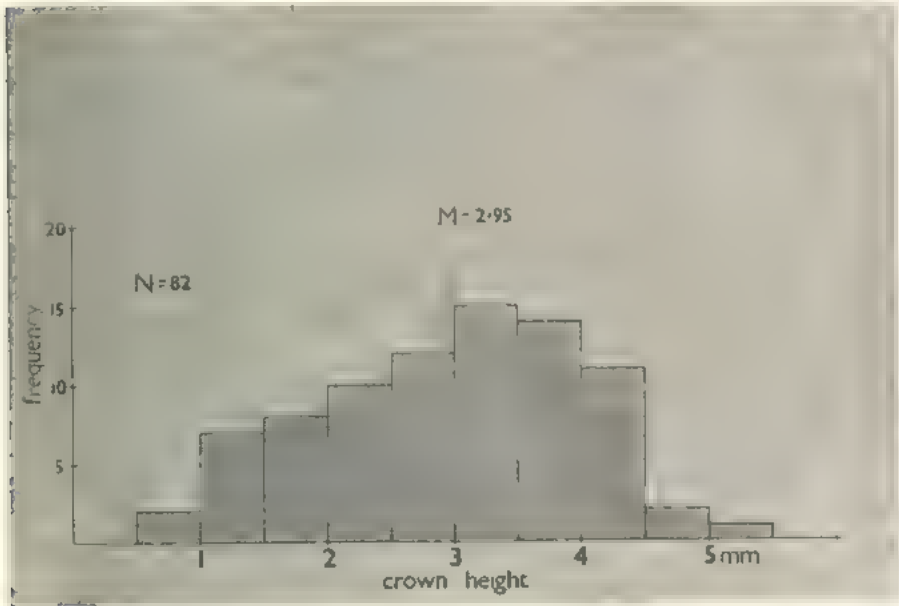


Fig. 11. Frequency distribution of tooth crown heights in *Allocodon leuckneri* gen. et sp. nov.

ginal denticles. Each crown was assigned to one or other of the 5 groups by straightforward visual inspection. Of the 158 crowns in the hypodigm 77 were badly damaged and could not be assigned with certainty to any particular group, the remaining 81 crowns were grouped as follows:

GROUP 1 (anterior premaxillary crowns) tall conical crowns, without marginal denticles	21 crowns
GROUP 2 (middle premaxillary crowns) tall conical crowns, with denticulate distal edge and simple mesial edge	4 crowns
GROUP 3 (posterior premaxillary crowns) conical crowns, taller than long, with denticles on both edges	10 crowns
GROUP 4 (anterior and middle cheek crowns) triangular crowns, about as high as long, with large denticles on both edges	31 crowns
GROUP 5 (posterior cheek crowns) triangular crowns, distinctly longer than high, with large denticles on both edges	15 crowns
Total	81 crowns

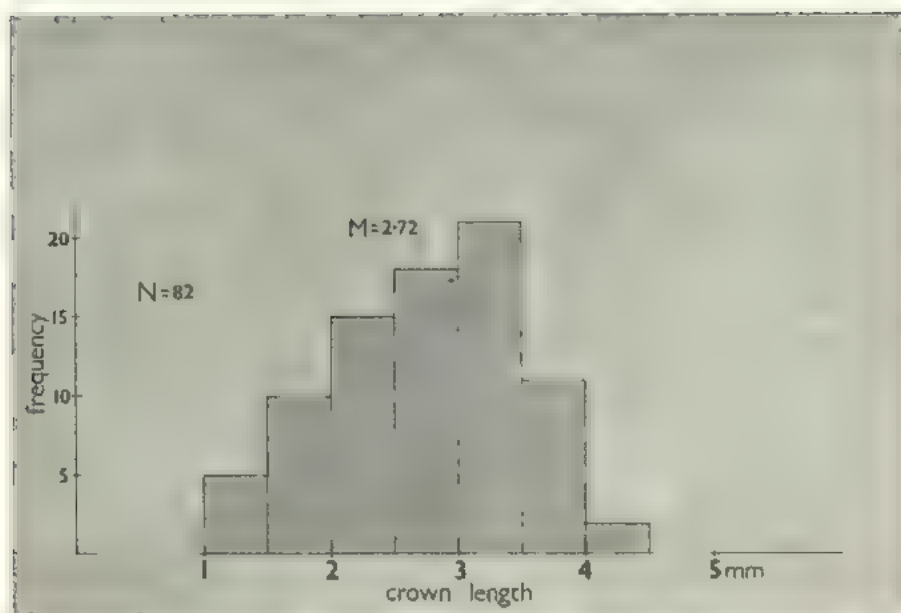


Fig. 12. Frequency distribution of tooth crown lengths in *Alorodon kachuet* gen. et sp. nov.

Groups 1 to 3 represent the premaxillary dentition, groups 4 and 5 represent the maxillary and mandibular dentitions.

Analysis of crown proportions and of marginal denticulation in each of these 5 groups yields the following figures:

	1	2	3	4	5
a) arithmetic mean for maximum crown height (mm)	3.4	3.9	2.9	3.0	1.9
b) arithmetic mean for maximum crown length (mm)	2.1	2.8	2.7	3.1	2.7
c) arithmetic mean for maximum crown height expressed as a percentage of maximum crown length (%)	159	138	113	95	68
d) arithmetic mean for number of denticles on mesial edge	0	0	3.5	4.1	3.9
e) arithmetic mean for number of denticles on distal edge	0	2.0	3.6	4.0	3.7
f) arithmetic mean for total number of denticles	0	2.0	7.3	8.0	7.5

The figures listed above are also expressed diagrammatically (figs. 14 and 15), together with indications of the observed range of variation in each group of crowns.

These simple analyses are however somewhat imperfect. Group 2, for example, consists of only four certainly assigned crowns (and one of these is damaged), made-

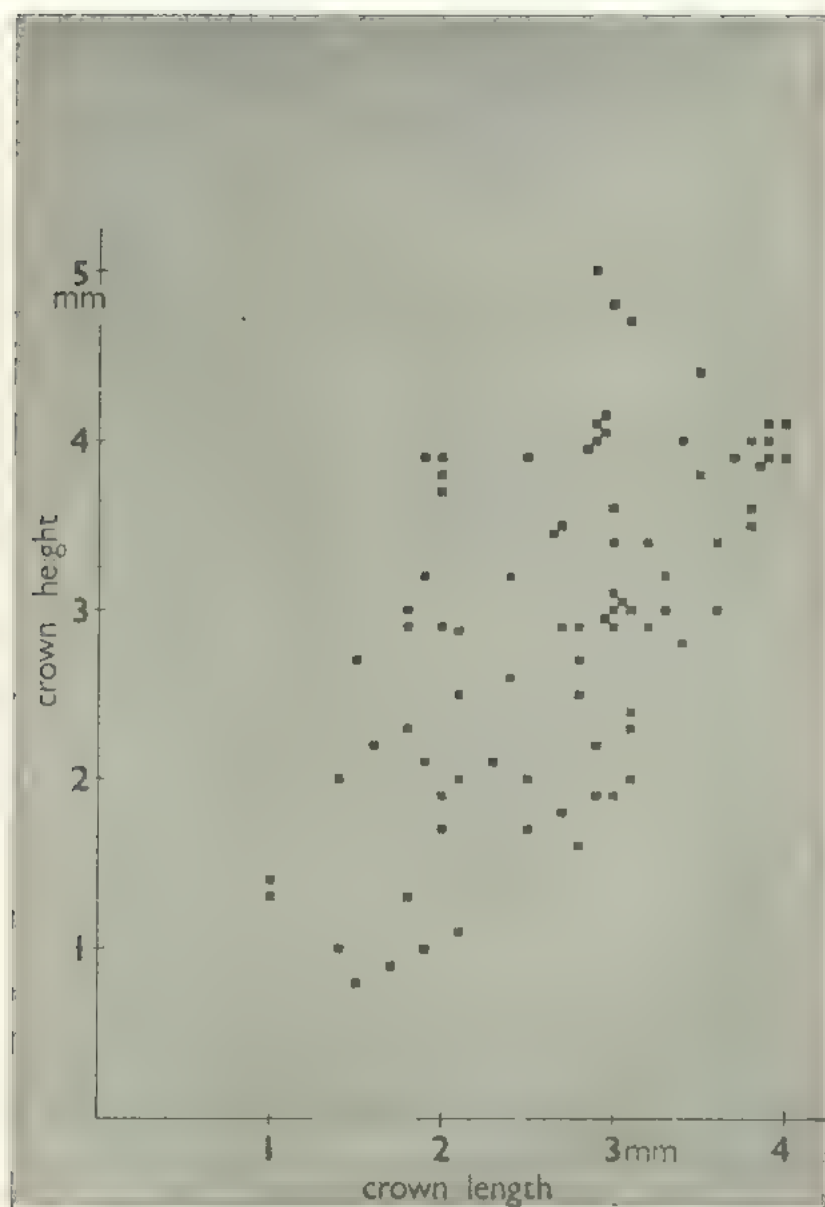


Fig. 13 Relationship between tooth crown height and tooth crown length in *Alveodon kuehnei* gen. et sp. nov.

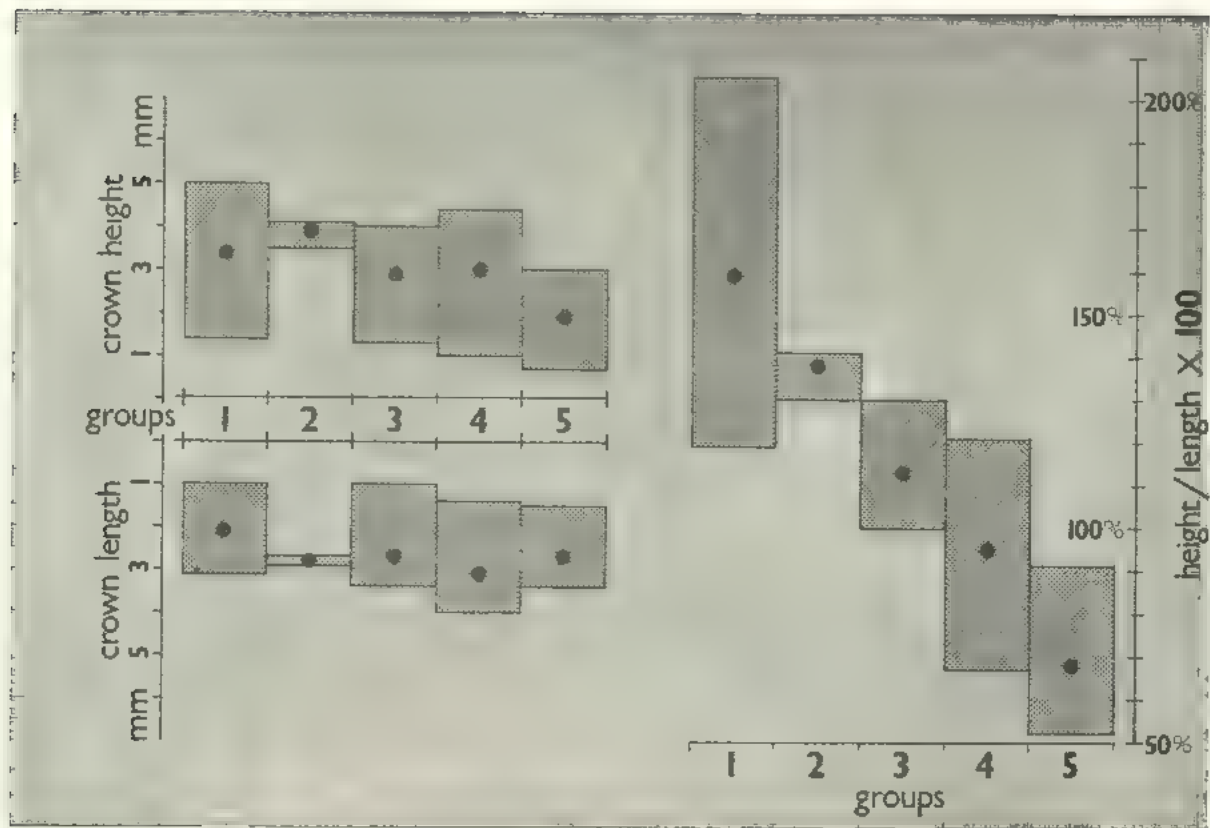


Fig. 14. An analysis of tooth crown proportions in *Alocodon kuehnei* gen. et sp. n. Column height indicates observed range of variation in each of the five groups of crowns. In each group the arithmetic mean is indicated by a dark spot.

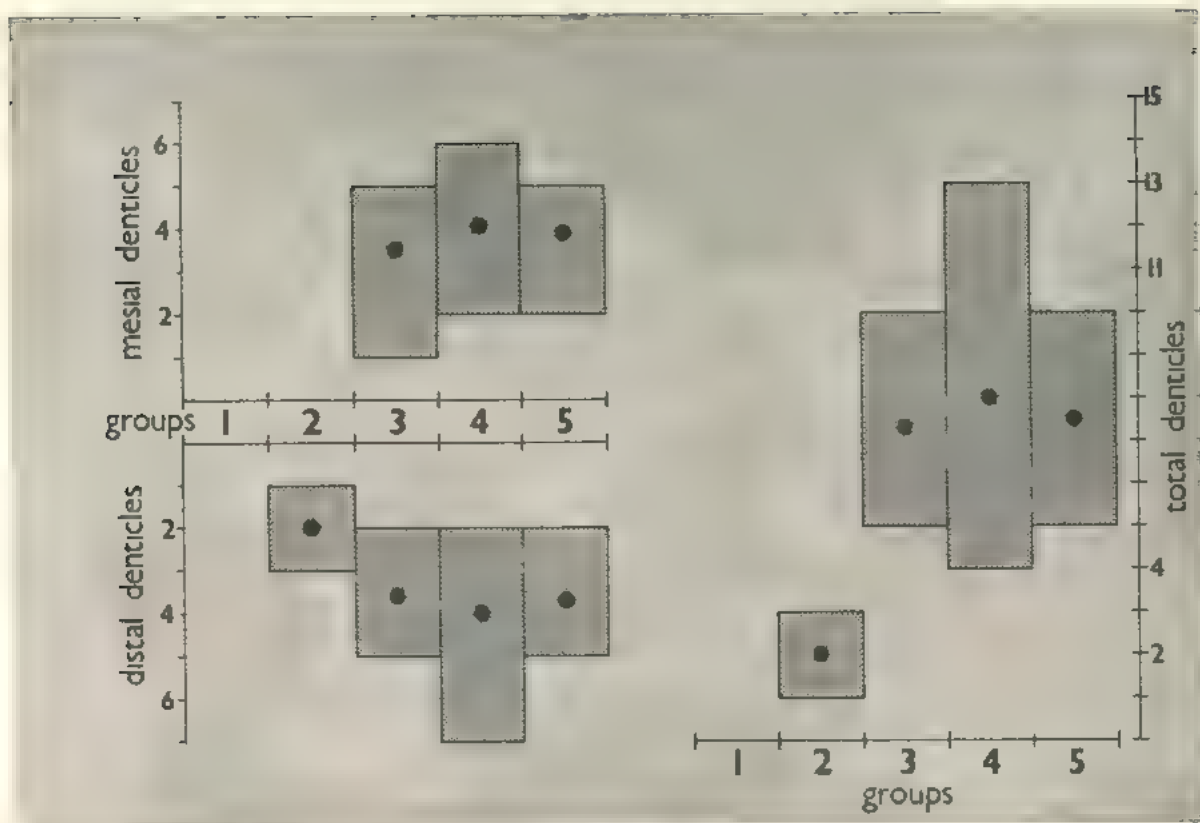


Fig. 15. An analysis of tooth denteculation in *Alopias kushneri* (gen. et sp. nov.). Columns show the observed range of variation in each of the five groups of groups. In each group the arithmetic mean is indicated by a dark spot.

quate numerical representation may well be a factor influencing the rather large figures for crown height and crown length in this particular group. Group 4 is represented by 31 crowns but is clearly a heterogeneous assortment. In the first place it includes both upper and lower crowns (as does group 5). Aside from this group 4 probably comprises three types of tooth crown: (a) «typical» cheek crowns (from the central parts of maxilla and dentary), (b) anterior «transitional» crowns (grading into the premaxillary crowns), and (c) posterior «transitional» crowns (grading into the depressed crowns of group 5). It has not proved possible to separate these three types of tooth crown.

Despite such imperfections groups 1 to 5 do seem to form a definite series (at least as far as crown proportions and numbers of marginal denticles are concerned). Groups 1 to 5 represent in effect, a backwards progression through the dentition of *Alcocodon kuehnei*. In this backwards progression a number of changes in tooth structure is readily observed. Figure 14 indicates that there is a slight, but perceptible decrease in crown height through groups 1 to 5. Crown length appears to remain fairly constant along the entire tooth row but may increase very slightly towards the rear. Figure 14 also demonstrates a correlation between crown shape and tooth site, anterior crowns are higher than long (and acutely conical) whereas posterior crowns are longer than high (and obtusely triangular in profile). Between these two extremes of crown shape (exemplified by groups 1 and 5 respectively) there appears to be an almost perfect gradation. Figure 15 shows that the number of marginal denticles per tooth tends to increase through groups 1 to 4 and then to decrease slightly in group 5.

Reconstruction of the dentition

The conclusions presented above permit reconstruction of the dentition, for they enable one to allocate crowns to particular sites in the jaws on the basis of crown shape and of marginal denticulation. The reconstruction (fig. 16) also utilises information from the dentitions of other hypsilophodontids.

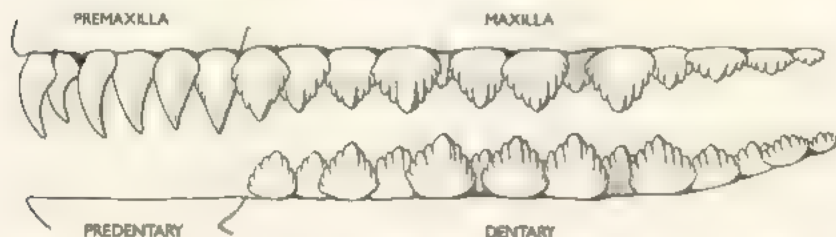


Fig. 16—*Alcocodon kuehnei* gen. et sp. nov. Left lateral view of the reconstructed dentition.

It has been assumed that the mandibular symphysis was formed by a toothless prementary bone and that teeth were implanted only in the premaxilla, maxilla and dentary. A similar arrangement obtains in other hypsilophodontids. The posterior extent of the prementary is, of course unknown; in the reconstruction this bone is shown reaching back almost to the suture between maxilla and premaxilla (i.e. it is intermediate in extent between the prementaries of the Triassic *Fabrosaurus australis* and of the Wealden *Hypsilophodon foxii*).

The next step in reconstructing the dentition is to estimate the numbers of teeth in the various jaw bones. *Fabrosaurus australis* and *Hypsilophodon foxii* are the only hypsilophodontids in which the dental formula is known in great detail and these two forms constitute the entire basis for analogies. The *Fabrosaurus* dentition comprises 64 to 68 teeth, of which up to 12 (18%–19% of the total) are located in the premaxillae (THULBORN, 1970a). GALTON (in press) figures the *Hypsilophodon* dentition with 62 teeth, of which 10 (16%) are sited in the premaxillae. One might reasonably expect any unbiased sample of 100 hypsilophodontid teeth to contain between 15 and 20 premaxillary teeth (the theoretical limits of occurrence — calculated as $Np = 3 \sqrt{Npq}$ and $Np \pm 3 \sqrt{Npq}$ — being 5 and 31) (*). But in the selection of 81 crowns from the hypodigm of *Alocodon kuehnei* (see preceding discussion) 35 crowns have been assigned origins in the premaxillae — i.e. 43% of the sample. If the sample is unbiased there are several factors which might account for this unexpectedly high proportion of premaxillary crowns. First, it is possible that *Alocodon kuehnei* did have a relatively large number of premaxillary teeth, it might conceivably have had more than 6 teeth in each premaxilla (the maximum recorded for a hypsilophodontid) but it is unlikely that these teeth were numerous enough to represent some 40% of the dentition. Second, it is possible that some crowns which are supposed to have come from the rear of the premaxilla (group 3) actually came from the anterior part of the maxilla. But even if one assumes that all the crowns in group 3 came from the cheek regions the percentage of premaxillary teeth in the sample still remains inordinately high (31%). Third there is the possibility that premaxillary teeth did constitute 15%–20% of the dentition but that these teeth were lost and replaced at a faster rate than the cheek teeth. This is not an unreasonable proposition when one considers the rather exposed position of the premaxillary teeth. EDMOND (1969) suggests that there is no continuity of the dental lamina across the maxilla-premaxilla suture in reptiles and there seems no reason why rates of tooth replacement should not differ in these two bones. But an unbiased sample with 43% premaxillary crowns would require the premaxillary teeth to be replaced twice as fast as the cheek teeth (assuming the dentition of *Alocodon kuehnei* to be of fairly normal hypsilophodontid type), this seems highly improbable.

Any of these factors (high premaxillary tooth count, misidentification of cheek teeth, differing rates of tooth replacement) may have contributed to the high proportion of premaxillary teeth in the sample. But such factors probably have a very small effect.

So it must be assumed that the sample of teeth from *Alocodon kuehnei* is biased. Many crowns in the sample are damaged in a way which suggests that they have suffered transport by rolling. Such transport may well have involved mechanical sorting of tooth types. The cheek crowns of *Alocodon kuehnei* approach more nearly to a spherical form than the conical premaxillary crowns and it is possible that some cheek crowns were winnowed out to leave an assemblage which is relatively rich in premaxillary crowns.

The «bias of identifiability», which is mentioned by SIMPSON and ROX (1939) must also be taken into account. The sample under consideration comprises 81 crowns which were selected from the hypodigm (158 crowns), and bias has undoubtedly entered the process of selecting this sample. The premaxillary crowns are readily identified and classified, damage may have removed the occlusal tip of the crown but this does not obscure the conical crown shape or reduce the number of marginal denticles (which are small and are in a sheltered position near the cervix). Broken cheek crowns are

(*) The lower limit of occurrence is calculated on the lowest recorded occurrence (16% in *Hypsilophodon*), the upper limit is calculated on the highest recorded occurrence (18% in *Fabrosaurus*).

much less easily classified, damage usually accounts for loss of the large marginal denticles and makes it difficult to estimate the original crown shape. In short, broken premaxillary crowns are more easily identified than broken cheek crowns, damage does not affect the criteria by which premaxillary crowns were sorted into groups 1, 2 and 3 but it does affect the single criterion (i.e. crown shape) by which cheek crowns were assigned to group 4 or group 5. This factor of 'identifiability' has certainly contributed to the seemingly large number of premaxillary crowns in the sample.

It is also worth noting that the hindmost cheek crowns resemble the teeth of hybodontid sharks such as *Acrodus* and *Hybodus*. This resemblance is so close that it has led to misidentifications. Professor KÜHNÉ and I have re-examined samples of fish teeth from Pedrogão and have discovered several cheek teeth of *Alocodon kuehnei*. Briefly, the posterior cheek crowns of *Alocodon kuehnei* may be distinguished from associated teeth of hybodontids by the following characters: (a) *lustre of enamel* (silky in *A. kuehnei*, shiny and glossy in hybodontids), (b) *ornament of ribs* (on one side only in *A. kuehnei*, but on both sides in hybodontids), (c) *cingula* (sometimes present in *A. kuehnei*, but never in hybodontids). The misidentification of posterior cheek crowns may also have contributed to the high proportion of premaxillary crowns in the sample.

Evidently the sample of teeth from *Alocodon kuehnei* is biased by a number of factors. Such a sample cannot safely be used to estimate the numbers of teeth in the various jaw bones and in reconstructing the dentition (fig. 16). I have necessarily had recourse to the dentitions of other hypsilophodontids. The premaxilla is shown with 6 teeth, the maxilla with 13 and the dentary with 14. The dental formula is closely comparable in the Upper Triassic *Fabrosaurus australis* and in the Wealden *Hypsilophodon foxii*. Numbers of maxillary and dentary teeth remain fairly constant throughout the family Hypsilophodontidae and the figures suggested for *Alocodon kuehnei* are probably quite accurate. But the number of premaxillary teeth is much more variable, the premaxilla of *Fabrosaurus australis* has up to 6 teeth whilst that of *Dysalotosaurus litorvorbecki*, from the Upper Jurassic of East Africa, is edentulous (JANENSCH 1955). The premaxillary crowns of *Alocodon kuehnei* are of three distinct types (non-denticulate with one edge denticulate and with both edges denticulate) and this variation in structure certainly implies that the premaxilla carried more than 3 or 4 teeth.

The diastema which separates the premaxillary and maxillary teeth in *Hypsilophodon foxii* (see GALTON, in press) would seem to be a specialization, neither *Fabrosaurus australis* nor the Purbeck *Echinosodon beckhami* (see OWEN, 1861b, Plate VIII fig. 1) has such a diastema and it has not been incorporated in the reconstruction of *Alocodon kuehnei*.

The cheek teeth were probably arranged in a simple row, rather than in complex batteries. The tooth rows have been reconstructed in irregular fashion, with large and small crowns mixed together, this irregularity is intended to convey some impression of waves of tooth replacement (*zahnreihen*) traversing the tooth rows.

Wear and replacement of the teeth

About one-fifth of the crowns in the hypodigm of *Alocodon kuehnei* bear distinct wear facets. Some wear facets may be attributed to interdental pressure, such facets occur on the mesial or distal margin and well away from the occlusal tip of the crown (figs. 1, 3 and 10). This wear indicates that the teeth were very tightly packed into the jaw bones. In some examples facets produced by interdental pressure extend on to the lingual or buccal face of the crown (fig. 6) and imply that the teeth were arranged *en echelon* or in roughly overlapping fashion (see reconstruction fig. 16). Overlapping of the teeth probably served three purposes: (a) to afford some pro-

tection to the periodontal membranes, (b) to prevent rotation of teeth in their sockets and (c) to increase the number of functional teeth in the jaws.

Some crowns show larger facets produced by tooth-on-tooth wear. These facets occur on the lingual faces of the maxillary crowns (fig. 6) and on the buccal faces of the mandibular crowns (fig. 9) and they are decidedly uneven in appearance - some are more steeply inclined than others - some are almost flat whilst others are concave from top to bottom (fig. 9). This irregularity of the wear facets may be correlated with tight packing and overlapping of the teeth. Evidently there was no fixed pattern of occlusion. In *Aloecodon kuhnei*, occlusion between the irregular upper and lower tooth rows would have produced a «crushing» effect in some parts of the jaws (with low-angle wear facets) and a «shearing» effect elsewhere (with steep wear facets).

Every tooth which is available lacks the root, and every well preserved specimen shows definite traces of resorption at the base of the crown. These facts seem to indicate that each tooth broke at the cervix once it had reached the end of its functional life: the crown would have been shed and the root was presumably resorbed. Similar processes of tooth loss have been described in mammal-like reptiles (KERMACK, 1956) and in the hypsilophodontid *Fabrosaurus australis* (see THULBORN, 1971a). KERMACK has suggested (op. cit.) that root resorption may have reduced the loss of calcium salts and might have assisted in preventing infection of the alveoli.

THE GUIMAROTA ORNITHISCHIAN

Phyllodon henkeli gen. et sp. nov.

LOCALITY

Map reference: Carta Militar de Portugal, Sheet 297 (Leiria), 0° 20' E., 39° 44' N. The locality is a small coal pit south of the town of Leiria. The fossiliferous rocks are lignitic marls and the history of collecting at this site has been described in detail by KÜHNLE (1968).

FLORAL AND FAUNAL LIST

PLANTAE

Chlorophyta

Porochorda raskyae (oogonia)

Porochorda westerbeekensis (oogonia)

PROTOZOA

Foraminifera

3 genera

MOLLUSCA

Gastropoda

8 genera

Lamelibranchia

5 genera

ARTHROPODA

Ostracoda

Bivalvocypris sp.

Celacella merina

Darwinia sp.

Leiria paucistriata

Lesia striata
Oerliana kammerdigiensis
Poisa clarea
Therapsynicum hamigymna
Therapsynicum wyomingense
Timonaxena mackerroni

Cirripedia
 1 genus

ECHINODERMA

Echinodonta
 Spinea

FISCES

Selachii
Acerodus sp.
Asieracanthus sp.
 Holostei
Lepidotes sp.
 8 other genera

AMPHIBIA

Urodela
 Anura

REPTILIA

Chelonia
 Shell fragments
 Squamata
Ecklesiastaurus hoffstetteri
Otenlogenys reedi
Intropisaurus pollicidens
Lisboaaurus estrei
Lisboaaurus mitternataus
Marcillostus cf. brodiei
Saurillus henckeli
Saurillus cf. obtusus
Saurillus praeformis
 Crocodilia
Machimosaurus hugli
 2 other genera
 Saurischia
Bohrispondylus sp.
 8 other genera
 Ornithischia
Phyllodon henckeli gen. et sp. nov.
 Pterosauria
Phodactylus sp. (teeth)
Rhamphochynchus sp. (teeth)

MAMMALIA

Decodonta
 3 genera
 Paurodontidae and Dryolestidae
 6 genera
 Multituberculata
 3 genera

The characean oögonia indicate an early Kimmeridgian age for the Guimarota horizon. KÜHNE (1968) points out that this age is supported by the evidence of the ostracod assemblage and gives a list of works dealing with the Guimarota locality and its fauna. Important works include those by KREBS on *Machimosaurus* (1967, 1968) and on the mammals (1969, 1971), and that by SEIFFERT (1970) on the lizards.

THE ORNITHISCHIAN TEETH

The Guimarota locality has yielded 56 ornithischian teeth. Only two of the teeth, which are black or dark brown in colour, retain roots, in every other case the base of the crown shows traces of root resorption. The teeth are generally well preserved but many are cleanly broken, only a few are rounded in a way that might suggest prolonged transport or rolling. The teeth vary considerably in size and in shape but there are, as in the case of *Alcodon kachneri*, good reasons to suppose that they represent a single species of ornithischian dinosaur.

SYSTEMATICS

Class REPTILIA

Order ORNITHISCHIA

Suborder ORNITHOPODA

Family HYPSILOPHODONTIDAE

Genus *Phyllodon* gen. nov.

Species *P. henckeli* sp. nov.

Etymology: Greek *phyllos* (a leaf) and *odon* (tooth) in allusion to the leaf-shaped cheek teeth. The specific epithet is to honour Dr SIEGFRIED HENKEL, who developed the collecting technique employed at Guimarota.

Type material: The holotype is a single cheek tooth crown (numbered G 5). A single premaxillary tooth crown (numbered G 2) is designated paratype.

Referred material: The hypodigm of *Phyllodon henckeli* comprises the holotype and the designated paratype together with 54 teeth or parts of teeth. All these specimens are preserved in the collection of the Lehrstuhl für Paläontologie at the Free University, Berlin.

Horizon and locality: All specimens were collected from lignitic marls of early Kimmeridgian age at the Guimarota mine, near Leiria, central Portugal.

Diagnosis (for genus and monotypic species): Ornithischian dinosaur with heterodont dentition. Tooth crowns fully and uniformly enamelled bucco-lingually compressed, higher than long, deflected lingually. Buccal faces of crowns smooth and convex, occasionally with shallow divergent furrows, lingual faces similar, but slightly flatter. Anterior premaxillary crowns broadly triangular, weakly recurved, without definite marginal denticles. Posterior premaxillary crowns similar in shape, but with small denticles on mesial margin (sometimes on distal margin in addition). Cheek crowns lozenge-shaped, higher than long, with bluntly rounded denticles which are deflected to the rear; marginal denticles grow larger away from the cervix, then decrease in size near occlusal tip of crown, occlusal tip formed by several small denticles. Definite cingula absent, but cheek crowns may carry a few small denticles at postero-internal margin.

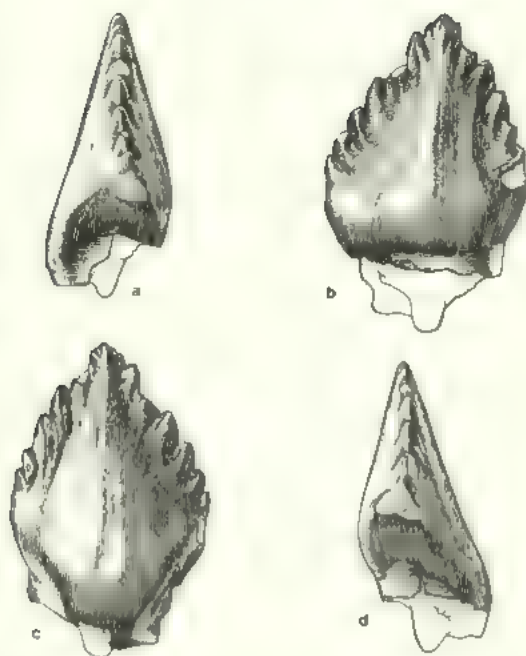


Fig 17 — *Phyllodon henckeli* gen. et sp. nov. Holotype. Crown of an anterior cheek tooth in mesial (a) lingual (b), buccal (c) and distal (d) views. $\times 14$.

DESCRIPTION

The premaxillary crowns are readily identified by their triangular shape and, in some cases, by their small marginal denticles the premaxillary crowns are described first and the remainder of the description refers to «cheek teeth» in general. Every crown in the dentition of *Phyllodon henckeli* seems to have been fully and uniformly enamelled.

The anterior premaxillary crowns are triangular in profile, bucco-lingually compressed and distinctly wider than long (see fig 18). Each crown is constructed at the cervix but lacks any trace of the prominent distal «shoulder» which is seen in the premaxillary crowns of *Alocodon kuchnei*. The distal margin is fairly thin and sharp and tends to a definite straightness. The convex mesial edge is somewhat thicker and may be elaborated into a series of feeble swellings (though none is distinct enough to be termed a denticle). Both buccal and lingual faces of the crown are smooth and rather featureless; the lingual face is slightly flattened (as it is in every crown of *Phyllodon henckeli*) and bears an extremely shallow groove at each margin. The material from Guimaraes includes at least 4 such anterior premaxillary crowns; these range in height from 1.7 mm to 4.0 mm.

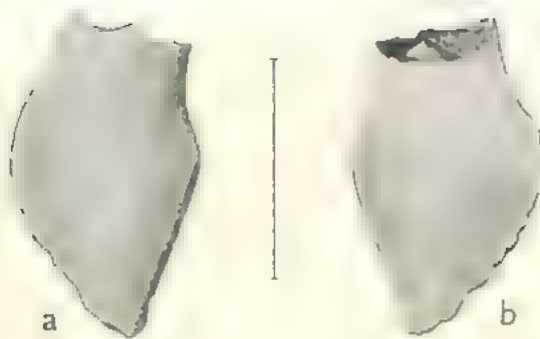


Fig. 18 — *Phyllodon henckeli* gen. et sp. nov. Designated paratype. Crown of a tooth from the anterior part of the left premaxilla in buccal (a) and lingual (b) views. Scale indicates 1 mm.

Crowns from the middle part of the premaxilla have several small denticles on their mesial edges (fig. 19b). Both buccal and lingual faces are marked with faint vertical furrows, the furrows are widely spaced and appear to be more strongly developed on the lingual faces of the crowns (particularly near the margins). It should be noted that this furrowing is always very weak and that it is in no way comparable

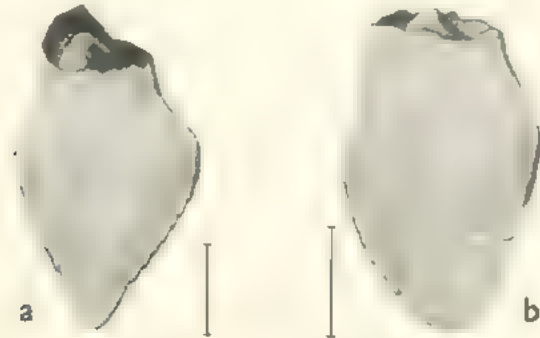


Fig. 19 — *Phyllodon henckeli* gen. et sp. nov. Lingual view of a crown from the posterior part of the left premaxilla (a). Lingual view of a crown from the middle part of the right premaxilla (b). Each scale indicates 1 mm.

with the ornament seen on the premaxillary crowns of *Alocodon kuchnei*. There are at least 5 such partly denticulate crowns in the material; they range in height from 2.0 mm (estimated) to 5.0 mm and have denticle counts such as 3-0, 4-0 and 5-0.

The hindmost premaxillary crowns merge imperceptibly with the anterior cheek crowns and it is difficult to draw any firm line of distinction between the two types. Nevertheless a few crowns can be assigned with a fair degree of certainty, to either the premaxilla or the cheek regions — mainly on the basis of their marginal denticle

ization. Any crown which shows marked disparity between the numbers of denticles on mesial and distal edges is almost certainly from the rear of the premaxilla (fig. 19a). Crowns which are generally similar in shape but which have approximately equal numbers of denticles on mesial and distal edges are probably from the anterior cheek region (fig. 17).

Every cheek crown appears to be higher than long there being no trace of the depressed posterior crowns which were encountered in *Alocodon kuchnei*. It seems that such depressed crowns were not present in the dentition of *Phyllodon henkeli* (though their absence might be attributed to the smallness of the sample which is available). Each cheek crown of *Phyllodon henkeli* is roughly lozenge-shaped in profile and is deflected to the rear. The edges of the cheek crowns are developed into large blunt and slightly divergent denticles. On each edge the largest denticles are found near the middle, those towards the occlusal tip of the crown and towards the cervix being distinctly smaller. The denticles are confluent with feeble ridges on the lingual and buccal faces of the crown (those on the lingual side being a little more pronounced). In each case the occlusal tip of the crown is formed by a cluster of small denticles. None of the crowns has any step-like cingulum, but some carry a few small denticles on the lingual face, close to the hindmost marginal denticle (fig. 17).

The root is preserved in two specimens. The better preserved example (fig. 20a-b) shows that the root is considerably taller than the crown and that it is almost perfectly straight. The root is bucco-lingually compressed and is barely constricted at the cervix.

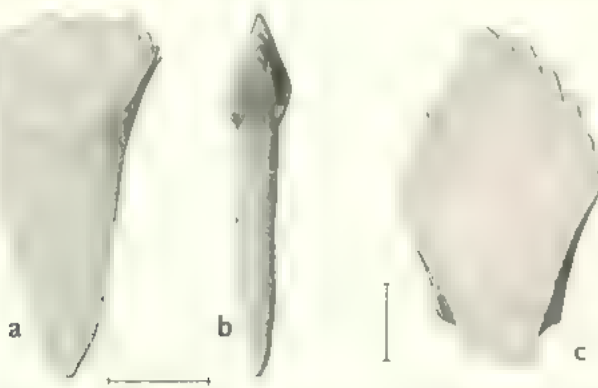


Fig. 20 — *Phyllodon henkeli* gen. et sp. nov. Buccal (a) and mesial or distal (b) views of a cheek tooth. Buccal view of a worn cheek crown (c). Each scale indicates 1 mm.

DISCUSSION

Systematic position

The denticulate and leaf-shaped cheek of *Phyllodon henkeli* are typically ornithoschian in appearance. The dentition resembles that of *Alocodon kuchnei* in its basic construction and there seems little doubt that *Phyllodon henkeli* is another hypsilophodontid. Assignment of the species to the family Hypsilophodontidae is warranted, once again by the well-differentiated premaxillary dentition.

Tooth crowns of *Phyllodon henckeli* may be distinguished without difficulty from those of *Alocodon kuehnei* — principally through their weaker ribbing and their lack of cingula. The premaxillary crowns are further distinguished by lacking any distal «shoulder» and by the straightness of the distal margin. The cheek crowns differ in shape (being higher than long), in the structure of the occlusal tip (a cluster of small denticles as opposed to a single large denticle), and in the radiating arrangement of the marginal denticles.

There seems to be no particularly close relationship between *Phyllodon henckeli* and *Alocodon kuehnei*. Indeed, certain features of the dentition set *Phyllodon henckeli* apart from all other hypsilophodontids. Perhaps the most distinctive of these features is the junction between the non-denticulate premaxillary teeth and the fully denticulate cheek teeth in *Phyllodon henckeli* marginal denticles appear first on the mesial edges of the premaxillary crowns, and then on their distal edges. This sequence of denticle development cannot be matched in any other hypsilophodontid in *Alocodon kuehnei* (and in *Fabrosaurus australis*) the marginal denticles are developed in reverse order. The relationships of *Phyllodon henckeli* within the family Hypsilophodontidae are examined more closely in the general discussion (see p. 126).

Structural variation in the dentition

The assumption that the ornithischian teeth from Guimarota represent a single species is sustained by a noticeable uniformity in structure. The teeth are all black or dark brown in colour, their crowns are fully and uniformly enamelled and the great majority of the teeth show traces of root resorption at the base of the crown. Every crown is higher than long and all but the premaxillary crowns are marked with feeble ribs arranged in a divergent pattern. None of the crowns has any definite cingulum.

Measurements of maximum crown height and of maximum crown length provide distributions approximating to normal (figs. 21, 22) and may be plotted to produce a closely coherent scatter (fig. 23). In addition a selection of crowns from the hypodigm may be used, as in the case of *Alocodon kuehnei*, to produce a realistic reconstruction of the dentition (fig. 24).

The teeth of *Phyllodon henckeli* show much less variation in structure than those of *Alocodon kuehnei*. Consequently it is difficult to assign individual teeth to particular sites in the jaws. The middle and anterior premaxillary crowns are readily distinguished by the lack of denticles on one or both edges (respectively), but it has proved impossible to draw any firm line of distinction between the hindmost premaxillary crowns and the cheek crowns. Nor is it possible to divide the cheek crowns into anterior and posterior types. In other words variation along the tooth row in *Phyllodon henckeli* cannot be investigated or described as thoroughly as it was in the case of *Alocodon kuehnei*. Nevertheless a general account is possible.

Crown height exceeds crown length along the entire tooth row in *Phyllodon henckeli*. There is no trace of the decrease in crown height, relative to crown length, which is observed in a backwards progression through the dentition of *Alocodon kuehnei*. If this backwards change in crown proportions does occur in *Phyllodon henckeli* it is certainly very insignificant and it has remained undetected. The surface ornament of the tooth crowns increases in strength towards the rear of the dentition. The anterior premaxillary crowns are practically smooth whilst the middle and posterior premaxillary crowns are marked with faint ribs and furrows. In the cheek crowns this ornament is even more pronounced, the ribs being confluent with the marginal denticles. None of the crowns has any true step-like cingulum, but some have a few small denticles on the lingual surface, close to the hindmost marginal denticle. Crowns which possess these

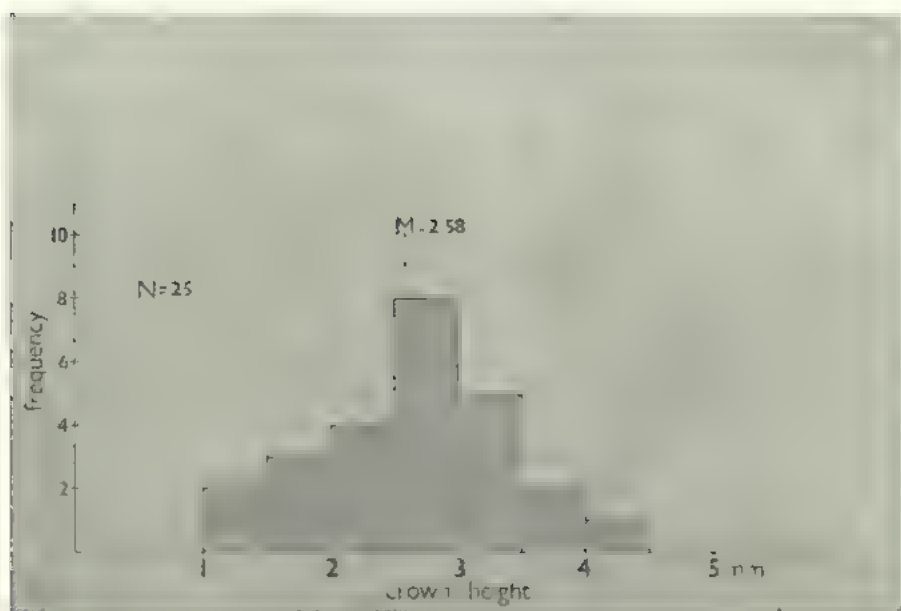


Fig. 21 — Frequency distribution of tooth crown heights in *Phyllodon henckesi* gen. et sp. nov.

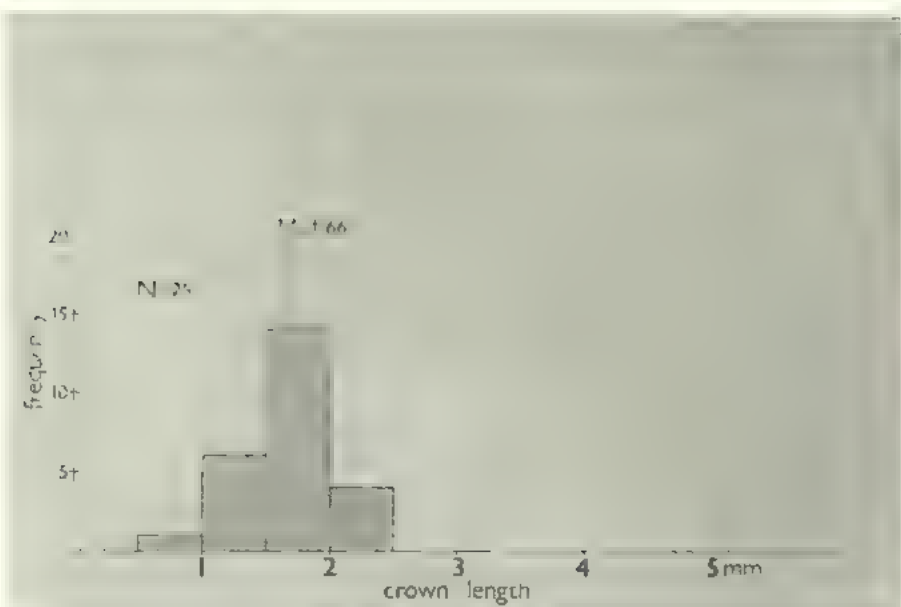


Fig. 22 — Frequency distribution of tooth crown lengths in *Phyllodon henckesi* gen. et sp. nov.

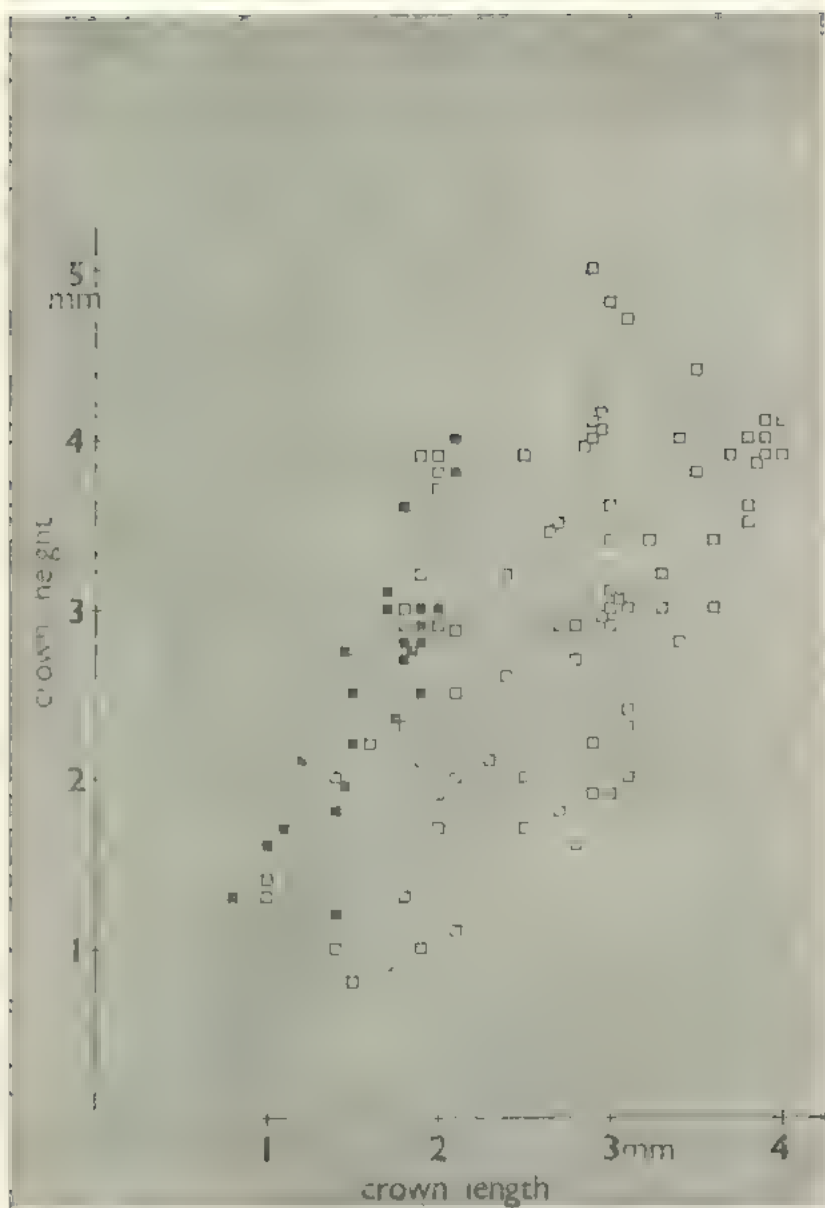


Fig. 23 Relationship between tooth crown height and tooth crown length in *Phyllodon henrichi* (solid squares) compared with the same relationship in *Alloceodon kuehnei* (open squares)

lingual denticles might tentatively be assigned to the anterior and middle cheek regions. Finally there is an increase in the number of marginal denticles per tooth from front to back in the jaws. But it cannot be determined if the number of denticles per tooth decreases slightly at the hindmost extremity of the tooth row (as it does in *Alocodon kuchnei*).

Reconstruction of the dentition

The dentition of *Phyllodon henkei* has been reconstructed (fig 24) using analogies with other hypsilophodontids. It must be emphasized that this reconstructed dentition is rather more conjectural than that given for *Alocodon kuchnei*. The speculative nature of the reconstruction stems from two factors, first the limited amount of evidence which is available and second the lack of any marked structural variation in the teeth (making it difficult to relate particular tooth types with specific sites in the jaws).

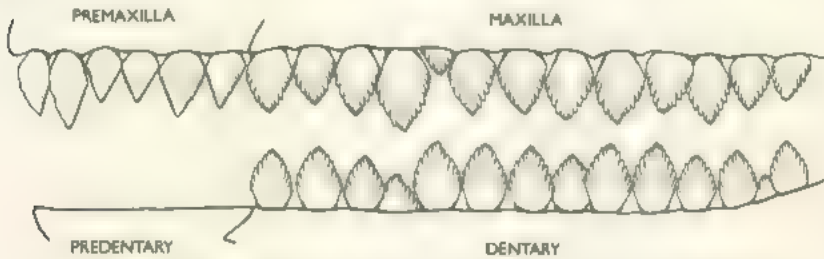


Fig 24 — *Phyllodon henkei* gen. et sp. nov. Left internal view of the reconstructed dentition.

The teeth of *Phyllodon henkei* are generally well preserved and appear to have suffered relatively little transport. In consequence it may be presumed that there was only slight preferential sorting of tooth types during transport and that the percentage of premaxillary teeth in the sample is a fair reflection of the proportion of such teeth in the entire dentition. Fifty-six tooth crowns have been examined. Three of these are merely fragments and cannot be assigned either to the premaxilla or to the cheek regions. Of the remaining 53 crowns 10 (i.e. 19%) are almost certainly from the premaxillae. In the Triassic *Fabrosaurus australis* 18%–19% of the entire dentition consists of premaxillary teeth and in the Wealden *Hypsilophodon foxii* the figure is 16%. The former has up to 8 teeth in the premaxilla (the maximum recorded in a hypsilophodontid) whilst the latter has 5, the dentition of *Phyllodon henkei* has been reconstructed with 6 teeth in the premaxilla. The premaxillary teeth are shown opposing a toothless premaxillary bone (designed to be intermediate in extent between the predentaries of *Fabrosaurus australis* and *Hypsilophodon foxii*). The maxilla is shown with 13 teeth and the dentary with 14; these figures are probably quite accurate since the numbers of teeth in maxilla and dentary remain fairly constant throughout the hypsilophodontids.

Wear and replacement of the teeth

Eleven crowns bear distinct wear facets. Only a few cheek crowns carry the small facets which may be attributed to interdental pressure (fig. 17). Such facets occur at the mesial or distal margin, well away from the occlusal tip of the crown, and their rarity implies that the teeth were not very tightly packed into the jaw bones. The facets produced by interdental pressure are very restricted in extent, in no case can they be traced on to the buccal or lingual surface of the crown. This indicates that the cheek teeth were disposed in a simple line, rather than in an overlapping series.

Broad, steeply inclined and almost flat wear surfaces, which are the product of occlusion, are much more common. Facets of this type are present on the lingual face of one premaxillary crown (fig. 19b) and are clearly the result of the tooth working against the horn-sheathed predentary. This particular tooth is of interest in that it shows two distinct wear facets — one superimposed upon and cutting into, an older one. This double wear may reflect spasmodic tooth eruption or it may point to damage and subsequent regrowth of the predentary. In some cheek crowns the facets produced by occlusal wear occur in pairs (fig. 20c) — an arrangement which suggests that occlusion involved interlocking between upper and lower teeth. The paired wear facets are not as regular as those which are observed in *Fabrosaurus australis* and in the Upper Cretaceous *Thecodontosaurus edmontonensis* (see THULBORN, 1971a). The steepness of the wear facets in *Phyllodon huxleyi* indicates that there was a pronounced «overbite» and points to a shearing (rather than crushing) action between upper and lower cheek teeth.

Tooth implantation is of normal thecodont type. Bucco-lingual compression of the roots would have prevented rotation of individual teeth within their sockets. Most of the crowns show definite traces of root resorption and it is likely that tooth loss followed the pattern which has been described for *Alcodon kuehnei*.

THE PORTO PINHEIRO ORNITHISCHIAN

Trimicrodon cuneatus gen. et sp. nov.

Hypsilophodon sp.

LOCALITY

Map reference: Carta Militar de Portugal, Sheet 349 (Lourinhã), 0° 13' W, 38° 13' N.

FLORAL AND FAUNAL LIST

PLANTAE

Charaeae

Porochara sp. (isogonia)

ARTHROPODA

Ostracoda

Isaulocyparis cf. palasapensis

Isaulocyparis sp.

Cetacella armata

Cetacella inermis

Cypridae sp.

REPTILIA

Ornithischia

Hypsilophodon sp.

Trimicrodon cuneatus gen. et sp. nov.

THE ORNITHISCHIAN TEETH

The Porto Pinheiro locality has yielded 4 ornithischian teeth. These teeth represent two distinct taxa.

Trimucrodon cuneatus gen. et sp. nov.

This ornithischian is represented by three small tooth crowns — the largest being barely 2 mm high. Two of the crowns show traces of root resorption on the adapical surface, the third is much rolled but retains part of the root. Each crown appears to have been fully and uniformly enamelled and is light yellow-brown in colour.

SYSTEMATICS

Class REPTILIA

Order ORNITHISCHIA

Suborder ORNITHOPODA

Family HYPSELOPHODONTIDAE

Genus *Trimucrodon* gen. nov.

Species *T. cuneatus* sp. nov.

Etymology. From the Latin *tri* (threefold) and *mucro* (point) in allusion to the three prominent denticles on each tooth crown. The specific epithet refers to the triangular shape of the tooth crowns.

Type material. The holotype is a single tooth crown (see fig. 25).

Referred material. The hypodigm of *Trimucrodon cuneatus* comprises the holotype together with two similar tooth crowns. All three specimens are preserved in the collection of the Lehrstuhl für Paläontologie at the Free University, Berlin.

Horizon and locality. All specimens were collected from the marls of late Kimmeridgian age at the headland of Porto Pinheiro, west coast of Portugal.

Diagnosis (for genus and monotypic species). Triangular and bucco-lingually compressed tooth crowns, about as long as high and slightly deflected to rear. Crowns fully and uniformly enamelled, with smooth faces. Lingual face a little flatter than buccal face. Mesial and distal edges almost straight, intersecting at right angles, ornamented with short blunt denticles which increase in size towards cervix. Foremost and hindmost of marginal denticles are strongly divergent, salient and sharply pointed.

DESCRIPTION

The description is based upon the holotype (fig. 25), the other crowns differing only in their poorer preservation and smaller size. All three crowns appear to have come from the cheek regions. The smallest and least well preserved example retains part of the root and indicates that tooth implantation was of normal thecodont type. In the other crowns the adapical surface is excavated into a crater and the root would seem to have been lost by resorption.

Each crown is broadly triangular in profile, about as high as long, and strongly compressed in a bucco-lingual direction. The lingual face is slightly flatter than the

buccal face, both faces are smooth and featureless, the sole ornament consisting of extremely fine vertical wrinkles in the enamel. Mesial and distal edges intersect at a right angle to form the obtuse occlusal tip of the crown. A slight arching of the mesial edge contrasts with the straightness of the distal edge and imparts a perceptible asymmetry to the crown. This asymmetry is emphasized by the backwards inclination of the occlusal tip. There are 6 denticles, which increase in size towards the cervix, on the distal edge. The most distal of these denticles is strongly divergent, salient and decidedly angular, it is confluent with a feeble ridge which extends for a short distance on to the lingual face of the crown. The other five denticles on the distal edge are shorter blunter and much less conspicuous. The denticles on the mesial edge resemble those on the distal edge but are slightly better defined.

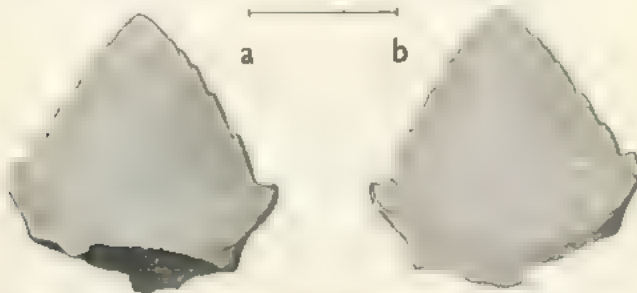


Fig. 25 *Trimucrodon cuneatus* gen. et sp. nov. Holotype. Crown of a cheek tooth in lingual (a) and buccal (b) views. Scale indicates 1 mm.

There are three small wear facets on the buccal face of the holotype. These facets are rounded in outline and are situated at the level of the salient foremost and hindmost denticles. The largest facet lies near the distal margin and the other two are close to the mesial margin. These steeply inclined facets may be attributed to interdental pressure and they indicate that the teeth were tightly packed into the jaw bones.

DISCUSSION

Systematic position

Trimucrodon cuneatus is referred to the order Ornithischia on account of its leaf-shaped and denticulate tooth crowns. Amongst the ornithischian dinosaurs *Trimucrodon cuneatus* may be compared most closely with *Echinodon becklesii* — a hypsilophodontid from the Purbeck beds of Dorset, England (1).

(1) *Echinodon becklesii* was originally described as a lizard (OWEN, 1861b) but comparisons with the Triassic ornithischian *Fabrosaurus australis* have shown that it is almost certainly a hypsilophodontid (see THILLOREN, 1970a). OWEN's account gives the type locality for *E. becklesii* as a 'thin fresh water stratum at Durdleston Bay, Isle of Purbeck'. In this area the Purbeck beds attain a thickness of nearly 400 feet and the horizon which yielded *E. becklesii* cannot be identified with certainty. It is possible that the material was collected from the 'Mammal Bed' at the base of the Middle Purbeck — this being a thin dirt bed which has yielded mammals and reptiles. But it seems more probable that *E. becklesii* was taken from somewhere within the Upper Building Stones.

The teeth of *Trimucrodon cuneatus* match the cheek teeth of *Echinodon beekleani* in nearly every respect. In both animals the tooth crowns are strongly compressed, triangular in profile, with an obtuse occlusal tip. In each case the crowns are fully and uniformly enamelled and they tend to a slight asymmetry (though this is not well shown in OWEN's figures (1861b) of *Echinodon beekleani*). The surfaces of the crowns are smooth and featureless in both animals. The teeth of *Trimucrodon cuneatus* have a very characteristic pattern of marginal denticulation and this is closely approached in *Echinodon beekleani* in each case the mesial and distal edges of the crowns are practically straight and are ornamented with denticles which decrease in size away from the cervix. The hindmost and foremost of the denticles are enlarged, salient and sharply pointed in both instances.

Detailed resemblances in tooth structure suggest that *Trimucrodon cuneatus* is a fairly close relative of *Echinodon beekleani*. It is on account of these similarities that *Trimucrodon cuneatus* has been referred to the family Hypsilophodontidae. The teeth of the two animals may be distinguished by a few differences in the style of the marginal denticulation. In *Echinodon beekleani* the denticles are very numerous and extend right to the occlusal tip of the crown. In *Trimucrodon cuneatus* there are fewer marginal denticles and these stop well short of the occlusal tip. The enlarged foremost and hindmost denticles are more strongly divergent in *Trimucrodon cuneatus*.

Hypsilophodon sp.

The second ornithischian from Porto Pinheiro is represented by a single specimen (fig. 28). This consists of a heavily worn tooth crown with part of the root still attached and it has a total height of 3 mm. Much of the crown has been removed by wear on the buccal side and it is difficult to estimate the original shape of the crown. The mesial margin of the crown runs straight into the root without interruption, but at the distal margin the crown swells into a rounded 'shoulder' just above the cervix. The root is slightly arched to the exterior and the crown retains a few patches of light yellow-brown enamel. The lingual face of the crown is rather flat and bears a feeble vertical rib near the mid-line. This rib is flanked by even weaker vertical ribs (three towards the distal margin and one towards the mesial). Planar wear surfaces extend right across the buccal face of the crown and clearly indicate that this is a lower tooth. The buccal surface carries two distinct wear facets, a broad and steeply inclined facet occupies that part of the crown adjacent to the cervix whilst a slightly steeper facet is present towards the occlusal margin. The two facets intersect in a straight line which runs down and forwards from the distal margin. This double wear may point to spasmodic eruption of the tooth alternatively it may reflect intermittent eruption, or replacement, of the opposing maxillary tooth.

Dr P. M. GALTON has made a thorough study (in press) of the Wealden *Hypsilophodon* fauna and assures me that the worn mandibular teeth of this animal are very similar indeed to the specimen from Porto Pinheiro. In each case the flattened lingual face of the tooth crown is ornamented with vertical ribs and the root is slightly arched to the exterior. Tooth wear is planar in both cases. The crown from Porto Pinheiro appears to have been fully enamelled, but it is not clear if the enamel was thicker

which overlies the 'Cinder Bed'. It would seem most reasonable to follow APPELBY et al. (1967) in referring *E. beekleani* to the Middle Purbeck, greater stratigraphic precision is not possible.

The illustrations provided by OWEN (1861b Plate VIII, figs. 1 to 8) are somewhat unreliable. Through the courtesy of Dr A. J. CHALK I have examined the material of *E. beekleani* in the British Museum (Natural History) and have found the following of OWEN's illustrations to be the least inaccurate: figs. 1, 1a, 2, 2a, 3, 3a, 3b and 4.

on one side of the tooth than on the other (as it is in *Hypsilophodon foxii*). The characteristic straightness of the mesial margin and the distinctive distal «shoulder» of the crown can also be matched in the lower cheek teeth of *Hypsilophodon foxii*. In view of these pronounced similarities (in tooth shape in tooth ornament and in tooth wear) the specimen from Porto Pinheiro has been referred to the genus *Hypsilophodon*. It would seem from the limited evidence which is available that the Porto Pinheiro *Hypsilophodon* is a fairly direct antecedent of *Hypsilophodon foxii* itself.

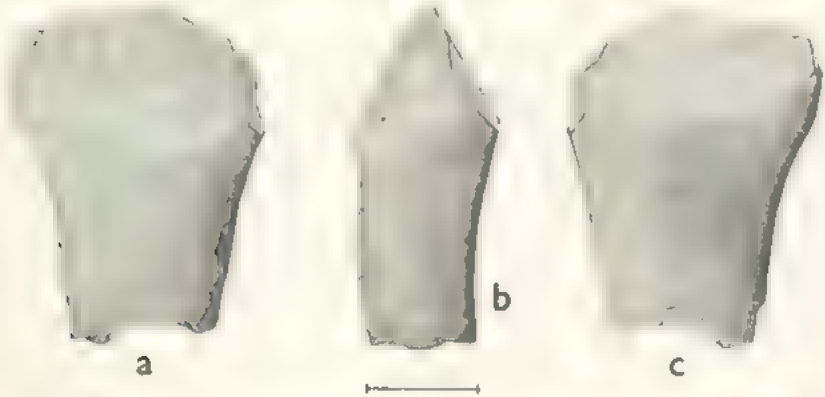


Fig. 26 *Hypsilophodon* sp. from the late Kimmeridgian of Porto Pinheiro. Worn tooth from the left dentary in lingual (a), mesial (b) and buccal (c) views. Scale indicates 1 mm.

DISCUSSION

The following is a complete list of the ornithischian dinosaurs which are at present known from Portugal:

- Alocodon kuhnelti* gen. et sp. nov.;
hypsilophodontid; Upper Jurassic.
- Hypsilophodon* sp.;
hypsilophodontid; Upper Jurassic.
- Phyllodon henkeli* gen. et sp. nov.;
hypsilophodontid; Upper Jurassic.
- Trimacrodon curvatus* gen. et sp. nov.;
hypsilophodontid; Upper Jurassic.
- Iguanodon mantelli* MEYER 1832,
iguanodontid; Lower Cretaceous.
- Dacentrurus armatus* (OWEN, 1875) (*Omosaurus*);
stegosaur; Upper Jurassic.
- Dacentrurus lennieri* (NOFCSA, 1911) (*Omosaurus*);
stegosaur; Upper Jurassic.
- Lusitanosaurus lissicus* LAPARENT & ZEYSZEWSKI 1957;
?stegosaur; Lower Jurassic.

The ornithischians from the Kimmeridgian of Porto Pinheiro (i.e. *Hypsilophodon* sp. and *Trimucrodon cuneatus*) are assigned to the family Hypsilophodontidae because their cheek teeth approximate very closely to those of undoubted hypsilophodontids (*Hypsilophodon* form and *Echinodon becklesii* respectively). The teeth of *Alocodon kachneri* and of *Phyllodon henkei* do not find such convincing counterparts among known hypsilophodontids and these two forms are referred to the Hypsilophodontidae on account of their well-differentiated premaxillary teeth. It may be pointed out that premaxillary teeth do occur in a few ornithischians apart from hypsilophodontids in pachycephalosaurids, in protoceratopsians and in the Cretaceous iguanodontid *Thescelosaurus edmontonensis*. But none of these ornithischians is very far advanced beyond the hypsilophodontid grade of organization and it seems safe to conclude that any ornithischian with premaxillary teeth is one of the «lower» ornithopods. On this basis it may be stated that *Alocodon kachneri* and *Phyllodon henkei* are certainly ornithopods, and while there is no incontrovertible proof that these forms are members of the Hypsilophodontidae they may be accommodated most conveniently and most logically, within this particular family.

Hypsilophodontids constitute the persistent and rather conservative basal stock of the ornithischian dinosaurs (ROMER 1945, THULBORN 1970a, GALTON 1971). This stock of hypsilophodontids ranges from the late Trias through the Cretaceous and is fundamental to the whole pattern of ornithischian history: it represents the ancestry, ultimately at least of groups as diverse as the hadrosaurs, pachycephalosaurids and ceratopsians. It has been suggested that this succession of hypsilophodontids at the core of ornithischian phylogeny might best be envisaged as a plexus, or rope in which each species represents a single strand (THULBORN 1971b). This concept of a plexus, rather than a simple linear series, lacks the implication that any one hypsilophodontid might be directly related to another (an important qualification, since the fossil record of hypsilophodontids is decidedly sporadic).

The ornithischians described in this paper permit some elaboration upon this theme of a hypsilophodontid plexus at the heart of ornithischian history and more important they give some clues to relationships and to evolutionary trends within the Hypsilophodontidae. In this context the stratigraphic setting of of Portuguese hypsilophodontids is particularly favourable: they are conveniently intermediate in age between the hypsilophodontids of the Cretaceous and the ornithopods which have recently come to light in the Trias (see THULBORN 1971b, for a review of these). A number of hypsilophodontids (*Dryosaurus* spp., *Laosaurus* spp., *Nanosaurus* spp.) are recorded from the late Jurassic and early Cretaceous of North America (GILMORE, 1925, LAM, 1911, MARSH 1877a, 1877b, 1878a, 1878b, 1894). Unfortunately these forms are still very poorly known and their systematics are in a most confused state, and until these ornithopods have been thoroughly revised they will be of little use in any study of relationships within the Hypsilophodontidae. In consequence it is necessary to consider the Portuguese hypsilophodontids apart from (and not in conjunction with) their North American contemporaries.

Before proceeding to investigate relationships within the Hypsilophodontidae it is desirable to establish criteria for assessing the closeness, or remoteness, of the relationship between any two hypsilophodontids. The degree of affinity between two hypsilophodontids might be reflected by pronounced resemblances, or pronounced differences, in the following characters:

- I) the extent of the premaxillary dentition;
- II) the transition between premaxillary and maxillary teeth;
- III) the structure of the cheek teeth;

- IV) the degree of change (if any) in crown shape from front to back in the cheek dentition.
- V) the pattern of tooth wear.
- VI) the presence or absence of cheeks.

These six characters are considered in turn.

1) The extent of the premaxillary dentition

The primitive condition, seen in the Upper Triassic *Fabrosaurus australis*, is that in which the premaxillary tooth row extends without interruption to the tip of the snout. More advanced conditions are seen in the Wealden *Hypsilophodon* form (where the premaxillary tooth row is preceded by a toothless space) and in the Upper Jurassic *Dysalotosaurus litton-vorbecki* (where the premaxilla is edentulous). Such variations in the extent of the premaxillary dentition may reflect different feeding mechanisms and different types of jaw action. In *Fabrosaurus* the crowded premaxillary teeth probably hit against the horn-sheathed predentary to produce an efficient «cropping» action. This food-gathering technique is paralleled (but in inverted fashion) in the living artiodactyls where the lower incisors bite against a horny pad in the upper jaw. In *Fabrosaurus* the anterior premaxillary teeth overhang the front of the predentary and would have prevented any protrusion of the mandible; this arrangement, together with evidence from worn teeth, indicates that the jaw action in this primitive hypsilophodontid was essentially vertical (THULBORN 1971a). In *Hypsilophodon* the abbreviated premaxillary dentition was probably preceded by a horny beak (supposing that at the mandibular symphysis) and in *Dysalotosaurus* this beak replaces the entire premaxillary tooth row. The acquisition of a premaxillary beak might have facilitated use of a prehensile tongue in food gathering: it would also have permitted some forwards sliding of the mandible to produce a grinding action between upper and lower cheek teeth.

It seems safe to conclude that any hypsilophodontid which retains a complete premaxillary dentition is a fairly direct descendant of the primitive Triassic hypsilophodontids (best exemplified by *Fabrosaurus australis*). On the other hand it is dangerous to infer that two hypsilophodontids are closely related because their premaxillary dentitions are reduced to the same extent. This is because the premaxillary dentition appears to have suffered reduction, or loss, at different times in several independent stocks of hypsilophodontids. The ornithomimid family Iguanodontidae is an artificial assemblage which probably arose from the hypsilophodontids through iterative phases of evolution (THULBORN 1971b). And since the iguanodontids (with the exception of *Thecodontosaurus edmontoniensis*) lack premaxillary teeth it is clear that each of their several lines of hypsilophodontid ancestry must have shown some independent trend towards loss of the premaxillary dentition.

2) The transition between premaxillary and maxillary teeth

In no hypsilophodontid is this transition in the upper dental series smooth and uninterrupted. There seems, without exception, to be some more or less obvious change in tooth structure across the premaxilla-maxilla suture. This changeover from non-denticulate premaxillary teeth to fully denticulate cheek teeth is accomplished in various ways. In *Fabrosaurus australis* this transition involves a change in crown shape (from conical to broadly triangular) combined with the gradual acquisition of marginal denticles: first on the distal edges of the crowns, and then on their mesial edges. The arrangement seen in *Fabrosaurus australis* seems to be the primitive one and it per-

sists in the Callovian *Alocodon kuehnei*. Other hypsilophodontids show different types of transition between premaxillary and maxillary teeth. In the Kimmeridgian *Phyllodon henckeli* there is a less marked change in crown shape and the marginal denticles make their appearance in reverse order (first on the mesial edges of crowns, and then on their distal edges). The Purbeck *Echinodon beeklesii* shows a very abrupt changeover from acute and non-denticulate premaxillary crowns to obtuse and fully denticulate maxillary crowns (see OWEN 1861b Plate VIII fig. 1). In *Hypsilophodon foxii* the premaxillary and maxillary crowns differ only slightly in shape but they are separated by a wide diastema (GALTON, 1970). There is no evidence to suggest that any one style of changeover between premaxillary and maxillary teeth has appeared in more than a single stock of hypsilophodontids. So it is not unreasonable to postulate a fairly close relationship between hypsilophodontids which show the same pattern of change in tooth structure at the premaxilla/maxilla suture.

III) The structure of the cheek teeth

The cheek teeth of hypsilophodontids have never been subjected to intensive study and a search of the literature might lead one to assume that there is a distressing uniformity of tooth structure within the Hypsilophodontidae. But this is not the case for the cheek teeth of hypsilophodontids show a diversity in structure which seems to be unrivalled among the lissosaurs. A detailed comparison of cheek tooth structure is probably the surest method for assessing the closeness, or remoteness of the relationship between two hypsilophodontids. This comparative approach is fundamental to the study of Mesozoic mammals and there is no reason why it should not be applied with equal vigour to the teeth of fossil reptiles.

In examining and comparing the teeth of hypsilophodontids there are numerous factors to be taken into account. The more important of these factors are indicated below.

Enamel. Most hypsilophodontids resemble the Triassic *Fabrosaurus australis* in having tooth crowns which are fully and evenly enamelled. But in *Hypsilophodon foxii* the enamel is exceptionally thick on the buccal faces of the maxillary teeth and on the lingual faces of the mandibular teeth elsewhere on the tooth crowns of *Hypsilophodon foxii* the enamel coat becomes very thin and may disappear (GALTON in press).

Crown shape. The cheek crowns are often triangular in profile (e.g. *Fabrosaurus australis*, *Echinodon beeklesii*). In other hypsilophodontids the crowns may be lozenge-shaped (e.g. *Phyllodon henckeli*) or ovate (e.g. *Laosaurus consors*). Crown height may exceed crown length or vice versa and in several forms (such as *Alocodon kuehnei*) the crowns may be higher than long in some parts of the dentition and longer than high elsewhere.

Crown margins. The mesial and distal edges of the crown may be straight, convex or concave. The two edges may be similar (to give symmetrical crowns like those of *Echinodon beeklesii*) or they may differ (as in the asymmetrical crowns of *Trimucrodon cuneatus*).

Surface ornament. The crown surfaces may be smooth or they may show an extremely fine wrinkling of the enamel (e.g. *Echinodon beeklesii*). In many cases the crowns are ornamented with ribs: these may be irregular and discontinuous (e.g. *Alocodon kuehnei*), roughly parallel (e.g. *Hypsilophodon foxii*) or divergent (e.g. *Phyllodon henckeli*). The ribs often vary in their strength and distribution but in many hypsilophodontids there is a pronounced vertical rib near the mid-line of each tooth (e.g. *Dysalotosaurus lettowvorbecki*). The style of ribbing may within a single dentition and it may even vary from lingual to buccal sides in a single tooth (as it does in *Alocodon kuehnei*).

Marginal denticles. These show considerable diversity in number, size and shape. The denticles may be divergent (e. g. *Phyllodon henckeli*) or parallel (e. g. *Echinodon becklesii*), they may remain constant in size along the crown margin (e. g. *Fabrosaurus australis*) or they may grown smaller towards the occlusal tip of the crown (e. g. *Trimacrodon cuneatus*). In some cases the denticles barely project beyond the crown margin but in others they are extended and salient (both types being found in a single cheek crown of *Echinodon becklesii*). The style of the denticulation may vary from tooth to tooth within the dentition (e. g. *Alocodon kuchnei*) or even from mesial to distal margins on a single crown.

Occlusal tip. The occlusal tip of the crown may be angular (e. g. *Trimacrodon cuneatus*) rounded (e. g. *Alocodon kuchnei*), or mucronate (e. g. *Dysalotosaurus lettow-vorbecki*) it may consist of a single large denticle (e. g. *Alocodon kuchnei*) or of a cluster of small denticles (e. g. *Phyllodon henckeli*).

Cingula. Some hypsilophodontid teeth are without cingula (e. g. those of *Echinodon becklesii*), but others may have cingula developed as «steps» in the crown surface or as rows of denticles (e. g. those of *Alocodon kuchnei*). Each cingulum is usually quite short, but in extreme cases a cingulum may extend right across the lingual face of a crown or may be represented only a single denticle. Where a crown has one short cingulum this is normally situated at the postero-internal margin (an arrangement which is of considerable use in orientating isolated crowns). There are often two short cingula on the lingual surface of a crown in such instances the cingula may be equally developed or (more commonly) that at the distal margin may be slightly stronger than its mesial counterpart. It should be noted that the size and appearance of cingula may vary from tooth to tooth in a single animal.

Any comparative study of hypsilophodontid cheek teeth should take into account all the characters mentioned above. It must be emphasized that several of these characters may show a considerable range of variation within a single dentition. And for this reason it is advisable to base comparisons upon complete dentitions (or, at least upon reliable reconstructions or large numbers of isolated teeth).

While it is possible that the teeth of distantly related hypsilophodontids might show some fortuitous resemblance in one or two characters (perhaps crown shape and crown ornament) it seems extremely unlikely that convergence alone could account for more than a few similarities in tooth structure. In other words, a passing resemblance between the cheek teeth of two hypsilophodontids might indicate some affinity or it might, equally well, be coincidental, but numerous and detailed points of similarity are almost certainly indicative of close relationship.

The value of these comparisons in elucidating relationships within the Hypsilophodontidae is best illustrated by an example. The ornithischian teeth from the Carnian marls of Pedrógão were, upon their discovery, provisionally designated as *Echinodon* (KÜTNE, 1971). Yet the cheek teeth of this animal differ from those of *Echinodon becklesii* in very many respects (in shape, in ornament, in the structure of the occlusal tip, in the style of marginal denticulation and in having cingula). This wealth of differences in cheek tooth structure implies that there is no particularly close relationship between *Echinodon becklesii* and the Pedrógão ornithischian (i. e. *Alocodon kuchnei*). And by means of similar comparisons it may be deduced that *Alocodon kuchnei* is more nearly related to *Fabrosaurus australis* and that the closest Portuguese relative of *Echinodon becklesii* is *Trimacrodon cuneatus*.

IV) Changes in crown shape from front to back in the cheek dentition

Where complete dentitions (or reliable reconstructions) are available it is possible to compare changes in crown proportions along the tooth row. Briefly there seem to be two distinct conditions among the hypsilophodontids. In the first of these the posterior cheek crowns are much longer (relative to their height) than the anterior cheek crowns. The second condition is that in which crown length remains fairly constant (relative to crown height) along the entire cheek tooth series.

The first of these conditions, where the cheek tooth row decreases in height posteriorly, is encountered in the Triassic *Fabrosaurus australis* (see THULBORN 1970a, fig. 3) and may be regarded as a direct inheritance from the thecodontian ancestors of the Ornithischia. This primitive condition persists in *Echinodon becklesii* (see OWEN, 1861b Plate VIII, figs. 3 and 5) and probably in *Alocodon kuehnei*. In these animals the jaw articulation is set nearly in line with the tooth row and the jaws would have closed with a scissors-like action. This shearing type of jaw action is patently ill-suited to herbivores such as the hypsilophodontids and the backwards decrease in crown height may be interpreted as an adaptation to remedy this situation. The backwards lowering of the tooth row would have ensured that upper and lower tooth rows met in parallel in spite of the scissors-like jaw action. This modification of the tooth row together with the retention of the primitive thecodontian-like jaw action, characterizes the more conservative members of the Hypsilophodontidae.

The second condition, where the cheek teeth are fairly constant in height is seen in advanced hypsilophodontids such as *Hypsilophodon formi* and *Dysalotosaurus lettow-vorbecki*. In these forms the jaw articulation is set well below the line of the tooth row in order to ensure parallel closure between upper and lower teeth — without the necessity for any backwards decrease in crown height. This modification which affects the jaw joint rather than the dentition may well have appeared independently in several progressive lines of hypsilophodontids.

V) Tooth wear

Traces of planar tooth wear are encountered in many hypsilophodontids. But more distinctive patterns of tooth wear, such as the paired wear facets attributed to interlocking between upper and lower teeth (see THULBORN, 1971a) may be identified in ornithischians which are only distantly related (e.g. the Triassic hypsilophodontid *Fabrosaurus australis* and the Cretaceous iguanodontid *Thescelosaurus edmontensis*). Resemblances in tooth wear cannot, therefore be taken as reliable indications of close affinity between hypsilophodontids. This contention is supported by observing that tooth wear may be extremely variable within even a single species of hypsilophodontid (e.g. *Alocodon kuehnei*).

VI) Cheeks

GALTON (1973) suggests that the acquisition of cheeks may account to a very large degree, for the successful history of the ornithischian dinosaurs. Evidently the Triassic hypsilophodontid *Fabrosaurus australis* lacked cheeks (the lateral faces of the maxilla and mandible being rather flat) and this primitive condition seems to have persisted in *Echinodon becklesii*. In more advanced hypsilophodontids the former presence of cheeks may be inferred from the development of a recess in the lateral face of the maxilla and of a counterpart shelf in the flank of the mandible

Of the six criteria discussed above one (i.e. the comparative study of tooth wear) is of little use in the investigation of hypsilophodontid interrelationships. Three others (the extent of the premaxillary dentition, the degree of change in tooth shape along the tooth row and the presence or absence of cheeks) may be used to distinguish conservative hypsilophodontids from their more progressive relatives. The remaining two criteria (comparative studies of cheek tooth structure and of the junction between premaxillary and maxillary teeth) are the most important since they give reliable indications of hypsilophodontid interrelationships at species level.

By means of these criteria it is possible to investigate relationships within the hypsilophodontid plexus which lies at the core of ornithischian phylogeny. It is proposed to examine the better known hypsilophodontids in turn and to indicate the probable relationships of each. These relationships are expressed in diagrammatic form (fig. 27).

Hypsilophodontids first appear in the late Trias. *Fabrosaurus australis*, from the Red Beds of southern Africa, is perhaps the best known of these early hypsilopho-

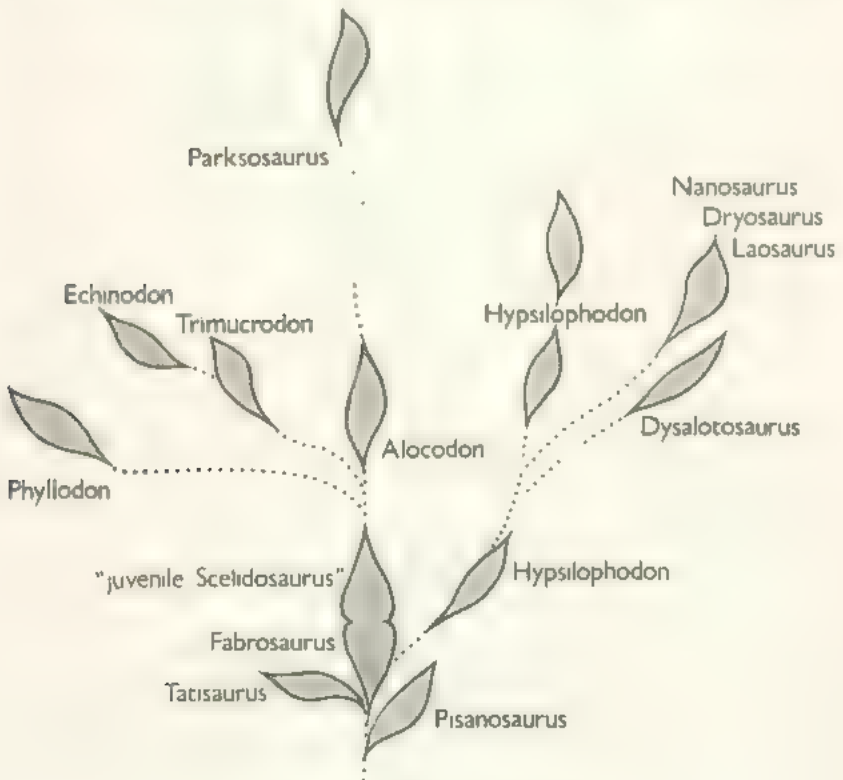


Fig 27 Relationships of the hypsilophodontids.

dontids and fulfils the role of a very useful ornithischian «archetype» (THULBORN 1970a, 1972). *Tafisaurus oehlerti*, from the late Trias of Yunnan, China is represented only by a fragment of jaw with the stumps of several teeth (SIMMONS, 1965). The relationships of *Tafisaurus* are obscure, but ROMER (1966) classifies it as a hypsilophodontid and it may be regarded, with some caution, as an ally of *Fabrosaurus*. *Pisanosaurus mertzi* is represented by teeth, cranial fragments and post-cranial bones from the Ischigualasto formation of Argentina (CASAMIQUELA, 1967). *Pisanosaurus* is still rather poorly known and is currently being restudied by Dr J. F. BONAPARTE, and until the results of this work are published it may be best to regard *Pisanosaurus* as a hypsilophodontid allied to *Fabrosaurus*. CASAMIQUELA's suggestion (1967) that *Pisanosaurus* should be separated from the hypsilophodontids at family level does not seem to be justified by the evidence which is at present available.

Several ornithopods from the late Trias of southern Africa (*Geranosaurus atavus*, *Lucorhinus anquetensis* and *Lucorhinus tucki*) have highly specialized dentitions which include very large «canine» teeth (see CROMPTON & CHANG, 1962; THULBORN 1970b). For the purposes of this paper and for the sake of brevity I have followed ROMER (1966) in excluding these forms from the Hypsilophodontidae.

NEWMAN (1968) has recorded fragmentary remains of a hypsilophodontid from the Lower Lias of Dorset, England. Certain of the limb bones are quite similar to those of the Wealden *Hypsilophodon foxi* and it may not be unreasonable to postulate a fairly direct relationship between the two forms. The species of *Hypsilophodon* which has come to light in the Kimmeridgian of Porto Pinheiro may then represent a very convenient intermediate. This succession of progressive hypsilophodontids, which culminates in *Hypsilophodon foxi*, seems to be quite distinct from the conservative central stock of the Hypsilophodontidae (which is represented by *Fabrosaurus* and its successors).

Parts of a second ornithischian from the Lower Lias of Dorset have been described and figured under the name «juvenile *Scelidosaurus*» (see RIXON 1968; ROMER, 1968; CHARRIG 1972). But this animal would seem from the published illustrations of its pelvic and hindlimb bones to be a fairly direct descendant of the Triassic *Fabrosaurus*.

Dysalotosaurus lettowortskyi, from the Tendaguru formation of East Africa, has edentulous premaxillae and cheek teeth which are not unlike those of iguanodontids (see JANENSCH 1955). *Dysalotosaurus* has often been regarded as an iguanodontid but the postcranial skeleton is decidedly hypsilophodontid-like in structure and I have followed GALTON (1971) in including *Dysalotosaurus* within the Hypsilophodontidae. The unusual dentition finds no exact counterpart in any other hypsilophodontid but the teeth and the skull are, on the whole, more like those of *Hypsilophodon* than those of *Fabrosaurus*. *Dysalotosaurus* probably represents a specialized divergence from the succession of already progressive hypsilophodontids which leads to *Hypsilophodon foxi* (though it might conceivably have arisen from the more conservative line springing from *Fabrosaurus*).

Alocodon karchni, from the Callovian of Pedrógão, has a dentition which resembles that of *Fabrosaurus* in many respects (even though the cheek teeth of the two animals are not immediately reconcilable in structure). Though its teeth do show a few specializations (such as denticulate cingula) *Alocodon* is probably not too far removed from the conservative main line of hypsilophodontid evolution. On the other hand *Phyllodon henckeli*, from the Kimmeridgian of Guimarães, seems to be more distantly related to this same conservative stock, for it shows a unique style of transition between premaxillary and maxillary teeth.

Pronounced resemblances in tooth structure point to a close relationship between *Trimucrodon cuneatus*, from the Kimmeridgian of Porto Pinheiro, and *Echmodon beek-*

less, from the Purbeck beds of Dorset. The persistence of primitive features (such as the high level jaw articulation) in *Echinodon* suggests that these two forms are not very remote from the hypsilophodontid stock which includes *Fabrosaurus* and *Alocodon*.

The hypsilophodontids which are recorded from the late Jurassic and early Cretaceous of North America (*Dryosaurus* spp., *Laosaurus* spp. and *Nanosaurus* spp.) cannot be discussed in any detail since their anatomy and their systematics are both far from clear. These forms are considered only for the sake of completeness, they are tentatively allied with the progressive hypsilophodontids leading to *Hypsilophodon* form (fig. 27) because the skulls of *Dryosaurus altus* and of *Laosaurus gracilis*, which are figured by GILMORE (1925), seem to resemble that of *Hypsilophodon*.

GALTON (1971) has suggested that the family Hypsilophodontidae may best be defined on the basis of limb proportions (the hypsilophodontids being characterized by elongated epipodial and metapodial segments in the hind limb). By this means the cursorial hypsilophodontids may be neatly separated from the graviportal iguanodontids. This scheme requires the transfer of the Upper Cretaceous *Thecosaurus* from the Hypsilophodontidae to the Iguanodontidae but permits retention of the contemporary *Parksosaurus* within the former family. *Parksosaurus* is separated from the rest of the hypsilophodontids by a very great hiatus in the fossil record. And this hiatus, which extends through the greater part of the Cretaceous period, makes it difficult to assess the relationships of the genus. *Parksosaurus* might best be regarded as a descendant from the conservative main line of hypsilophodontid evolution (though it might possibly have been derived from the progressive line which includes *Hypsilophodon*).

The whole of the preceding discussion may be condensed into a single diagram (fig. 27). The most firmly established part of this phylogeny is the line which includes, or leads to, *Fabrosaurus*, *Alocodon* and *Echinodon*. The more progressive line which includes *Hypsilophodon* seems to be quite distinct, it certainly extends back into the Upper Jurassic and may possibly have made its appearance as early as the Lower Liass.

Finally, it must be emphasized that the fossil record of the Hypsilophodontidae is very discontinuous. The hypsilophodontid interrelationships which are outlined above are mostly very tentative and it is likely that future discoveries will lead to modifications in the phylogeny which has been suggested.

SUMMARY

The application of specialized palaeontological techniques has brought to light a number of small dinosaurs in the Upper Jurassic of Portugal. This paper deals with four of these dinosaurs. These are referred to the family Hypsilophodontidae of the order Ornithischia and they are represented only by isolated teeth. The earliest of the Portuguese hypsilophodontids comes from the Callovian at Pedrógão, this animal, (*Alocodon kuehnei* gen. et sp. nov.) seems to be a fairly direct descendant of the Triassic *Fabrosaurus australis*. The second hypsilophodontid (*Phyllodon henckeli* gen. et sp. nov.) was discovered in the early Kimmeridgian of Guimarães and seems to represent a rather specialized divergence from the main line of hypsilophodontid evolution. The two remaining dinosaurs come from the late Kimmeridgian of Porto Pinheiro. The first of these (*Trimucrodon cuneatus* gen. et sp. nov.) is probably a close relative of *Echinodon becklesii* from the English Purbeck. The other is a species of *Hypsilophodon* which is directly antecedent to the Wealden *Hypsilophodon* form. Though these Portuguese fossils are very fragmentary they do permit critical reappraisal of relationships, and of evolutionary trends, within the hypsilophodontid plexus at the heart of ornithischian history.

RÉSUMÉ

L'emploi des techniques paléontologiques spécialisées a fait connaître plusieurs petits dinosauriens dans le Jurassique supérieur du Portugal. Cette étude s'occupe de quatre de ces dinosauriens. Ces animaux appartiennent à la famille Hypsilophodontidae de l'ordre Ornithischia et ils sont représentés seulement par les dents isolées. Le plus ancien des hypsilophodontidés portugais provient du Callovien à Pedrógão; cet animal (*Alcodon kuehnei* gen. et sp. nov.) paraît descendre en ligne assez directe de *Fabrosaurus australis* du Trias. Le deuxième hypsilophodontidé (*Phyllodon henkeli* gen. et sp. nov.) s'est découvert dans le Kimmeridgien inférieur à Guimarães et paraît indiquer une divergence plutôt spécialisée de la grande ligne d'évolution parmi les hypsilophodontidés. Les deux dinosauriens de reste proviennent du Kimmeridgien supérieur à Porto Pinheiro. L'un d'entre eux (*Trimucrodon cuneatus* gen. et sp. nov.) est vraisemblablement une forme voisine d'*Echinodon becklesii* du Purbeck d'Angleterre. L'autre est espèce d'*Hypsilophodon* qui est antécédent assez direct d'*Hypsilophodon foxii* wealdien. Quoique ces fossiles portugais sont très fragmentaires ils admettent l'appréciation critique des liens, et des cours évolutifs, dans le plexus hypsilophodontidé au cœur de «l'arbre généalogique» des Avipélviens.

RESUMO

A utilização de técnicas paleontológicas especializadas levou à descoberta de alguns dinossauros pequenos no Jurássico Superior de Portugal. Este artigo trata de quatro destes dinossauros. Estes pertencem à família Hypsilophodontidae da espécie Ornithischia e são tipificados somente pelos dentes isolados. O mais antigo dos hypsilophodontídeos portugueses vem do Caloviano de Pedrógão; este animal (*Alcodon kuehnei* gen. et sp. nov.) parece descender bem directamente do *Fabrosaurus australis* triásico. O segundo hypsilophodontídeo (*Phyllodon henkeli* gen. et sp. nov.) foi descoberto no Kimmeridgiense antigo de Guimarães, e parece simbolizar uma divergência um tanto especializada da linha principal de evolução dos hypsilophodontídeos. Os dois outros dinossauros são do Kimmeridgiense Superior de Porto Pinheiro. O primeiro destes (*Trimucrodon cuneatus* gen. et sp. nov.) é provável que seja parente próximo do *Echinodon becklesii* do Purbeck inglês. O outro é uma espécie de *Hypsilophodon* que é um antecedente directo do *Hypsilophodon foxii* wealdiano. Embora estes fósseis portugueses sejam muito fragmentários, permitem uma nova avaliação crítica de parentescos e de tendências evolucionárias, dentro da tela hypsilophodontídeo ao centro da história de Ornithischia.

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Since this paper went to press (1972) there has been considerable revision of views regarding the classification of ornithopod dinosaurs. Most importantly, GALTON (1972) has advocated separation of *Fabrosaurus australis* and its relative *Echinodon becklesii* into a new family (Fabrosauridae) on the grounds that these forms lacked the fleshy cheeks which were presumably present in the great majority of ornithischian dinosaurs.

Alcodon kuehnei and *Trimucrodon cuneatus* appear to be relatives of *Fabrosaurus australis* and *Echinodon becklesii* (respectively) and might best be referred to the family Fabrosauridae. The species of *Hypsilophodon* reported from Porto Pinheiro should clearly be retained in the family Hypsilophodontidae (s. s.). The systematic position of *Phyllodon henkeli*, from the Guimarota lignite, is not immediately obvious. From the preponderance of crown height over crown length along the entire dental series of *P. henkeli* it may be deduced that the jaw articulation lay well below the level of the cheek teeth. This low-level jaw articulation is matched in hypsilophodontids (s. s.) but not in fabrosaurids (where the jaw joint is at the level of the tooth rows). On the basis of this (admittedly slight) evidence I would recommend retention of *P. henkeli* in the family Hypsilophodontidae (s. s.).

The systematic position of *Lusitanosaurus haseius* may also be reviewed. It transpires that the (presumed) relative of *L. haseius*, the English *Scelidosaurus harrisonii*, may be an ornithopod — rather than an ankylosaur or a stegosaur (see THULBORN, 1974).

I present an updated classification for the ornithischian dinosaurs of Portugal:

SUBORDER ORNITHOPODA

Grade DOLICHOPODA

Family Fabrosauridae

Alcodon kushnei (Upper Jurassic)

Trimucrodon cuneatus (Upper Jurassic)

Family Hypsilophodontidae (s. s.)

Hypsilophodon sp. (Upper Jurassic)

?*Phyllodon henkeli* (Upper Jurassic)

Grade BRACHYPODA

Family Scelidosauridae

?*Lusitanosaurus haseius* (Lower Jurassic)

Family Iguanodontidae (s. s.)

Iguanodon mantelli (Lower Cretaceous)

SUBORDER STEGOSAURIA

Family Stegosauridae

Dacentrurus armatus (Upper Jurassic)

Dacentrurus lensleri (Upper Jurassic)

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